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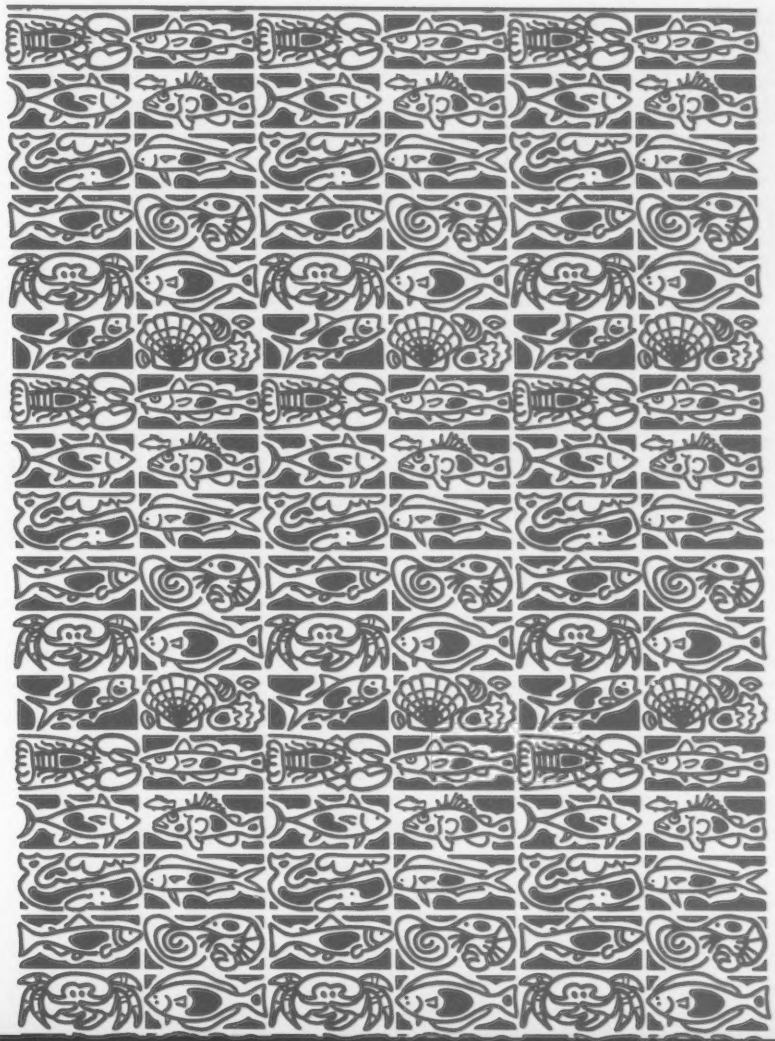

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Age and growth of larval Atlantic herring, *Clupea harengus*: a comparative study

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Abstract.—Age and growth of 1,746 Atlantic herring, *Clupea harengus*, larvae collected in the Nantucket Shoals–Georges Bank region during the autumn–winter seasons of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94 were determined by enumerating the daily growth increments of their sagittal otoliths. Growth with respect to length for each of the years was best described by a Gompertz curve. Owing to severe weather events in November, January, and February of the 1976–77 season which disrupted the fishes' feeding regimen, growth was much slower (0.16 mm/d) than in more recent years. Lower daily food consumption was reflected in the rapid and continual decrease in otolith diameter during the autumn and winter of 1976. Growth for the other six years was strong, showed only minor interseasonal fluctuations (0.22–0.24 mm/d), and ranged intraseasonally from a high of just over 0.40 mm/d in October to a low of 0.04 mm/d in February.

A general model of larval herring growth was constructed with data from six recent field seasons. Inverse regressive methods were employed to generate a composite growth curve with confidence limits for predicting age (days) for a given standard length (mm) from hatching until the onset of metamorphosis.

Analysis of otolith growth revealed a dramatic increase in the growth rate of the lapillus at about 2.5 months (29.0 mm). It is suggested that this increase may coincide with, or immediately follow, the filling of the otic bullae with gas and may provide an easily obtainable marker for estimating the timing of this critical event. The importance of this phase in the life of larval herring is discussed, particularly with reference to the 1976–77 season.

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Based on the general assumption that fluctuations in the year-class strength of fish stocks are often determined by the rate of mortality during the first year of life (Hjort, 1914; May, 1974; Sissenwine, 1984), ichthyoplankton surveys have been conducted in the Nantucket Shoals–Georges Bank region for more than twenty years. From 1971 to 1979, research cruises designed to gain a better understanding of the early life history of Atlantic herring, *Clupea harengus*, and its relationship to recruitment and spawning stock size were undertaken monthly throughout the autumn and winter. These surveys were coordinated by the International Commission for the Northwest Atlantic Fisheries (ICNAF). The United States participation in the program was conducted concurrently as part of the MARMAP (Marine Resource Monitoring, Assessment, and Prediction) program of the Northeast Fisheries Science Center (Sherman, 1980). The MARMAP program was designed to measure long-term changes in the variability of larval fish abundance off the Northeast coast of the United States and is ongoing.

In the 1970's, intense fishing pressure by distant-water fleets led to a steady decrease in herring abundance on Georges Bank (Anthony and Waring, 1980). Estimates of initial larval abundance declined by 95% from 1975 to 1976 (Lough et al., 1985). Herring populations in the region began to increase once again in the late 1980's, and this trend has continued into the 1990's (Smith and Morse, 1993). An examination of the age and growth of herring larvae, based on the enumeration of daily otolith increments, was initiated in 1976 (Lough et al., 1982). To understand better the recovery of Atlantic herring in the Georges Bank area, microstructural analysis of larval otoliths was incorporated as a routine procedure for each season beginning in the autumn of 1988. To date, otoliths from more than 1,700 larvae have been aged.

The primary goal of this study was to construct an age-at-length curve and a key for field-caught Atlantic herring larvae that describe their growth from hatch until onset of metamorphosis. Additionally, we compared larval growth during the autumn and winter of 1976–77 with that during six recent seasons of 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94. Otolith growth was analyzed to determine whether changes in the fishes' daily food rations, attributable to severe weather, could be de-

tected (Methot, 1983; Karakiri et al., 1989; Maillet and Checkley, 1991). Estimated standard lengths at hatching and metamorphosis were calculated and compared.

We also examined how developmental changes in the acoustico-lateralis system might relate to sensory thresholds that are critical in predator avoidance. Larval herring begin to demonstrate their characteristic C-shape startle response to environmental stimuli at a length of approximately 27–30 mm SL (Batty, 1989). This behavior does not become fully functional until the otic bullae are filled with air (22–30 mm), the air bladder and its connection to the acoustico-lateralis system are complete, and the larvae acquire the ability to swallow air at the surface (30–40 mm). Blaxter and Fuiman (1990) state that "filling the bullae with gas is probably the most significant event in the development of the anatomy of the sensory systems so far as predator evasion is concerned." They observed that successful attacks by predators were reduced from 77% to 32% following the filling of the bullae. Without a mechanism to adjust the volume of air with pressure changes, the fish are restricted in their ability to migrate vertically, limiting their ability to search for prey, to avoid predators, and to control transport (Hoss et al., 1989). Because it is virtually impossible to determine the condition of the otic bullae in field-collected larvae, the otolith to fish-length relationship was analyzed to determine its usefulness in estimating the timing of this critical developmental landmark.

Methods

Atlantic herring larvae were collected on 24 cruises at selected stations within a standard grid of sampling stations covering the western Gulf of Maine, Georges Bank, and Nantucket Shoals during the autumns and winters of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94 (Fig. 1; Table 1). The samples were collected with a continuous double-oblique haul by using a 61-cm bongo net sampler (0.505- and 0.333-mm mesh) deployed to a maximum depth of 200 m (100 m in 1976–77) or to within 5 m of the bottom in shallower areas. Further details of the sampling gear and protocols can be found in Posgay and Marak (1980) and Sibunka and Silverman (1984). Atlantic herring larvae were removed for otolith analysis immediately following the haul and preserved in 95% ethanol.

In the laboratory, larvae representative of the size-range collected were selected for analysis. Standard length was measured to the nearest 0.1 mm prior to removal of the otoliths. Differential shrinkage with respect to standard length was corrected by using Theilacker's (1980) algorithm, which was specified and discussed in Bolz and Lough (1983). The 2 sagittae and 2 lapilli were dissected from each fish and mounted whole on microscope slides with Permount. The growth increments on most of the otoliths were discernible without any further preparation.

The sagittae were viewed under a Zeiss compound microscope with transmitted light. The number of

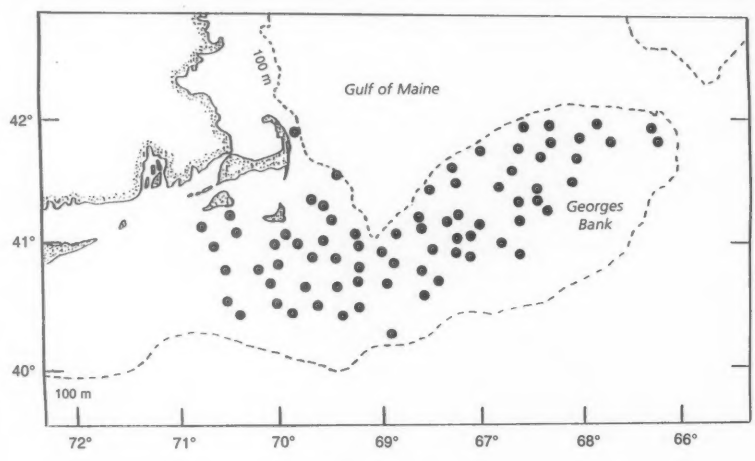

Figure 1

Station locations in the Gulf of Maine–Georges Bank region where larval herring were collected for otolith ageing.

growth increments were counted from the image projected by a drawing tube onto a Hewlett-Packard graphics tablet interfaced with an HP-87 microcomputer. All counts were made at a magnification of 800×. Three counts were made on one sagitta from each larva, and those otoliths with a repeatable increment count of >90% were used in the growth analysis. The other sagitta was counted once for comparison. Campana et al. (1987) found that detection of increments during the first 15–20 days posthatch are probably too fine to be resolved. In a previous study by Lough et al. (1982), it was found that the mean age of a 3-increment larva was approximately 22 d; consequently, a correction factor of 19 was added to the number of increments recorded in order to establish each larva's estimated age in days from hatch (Stevenson et al., 1989; Townsend et al., 1989). Measurements of the anterior–posterior diameters (otolith length) of the sagittae and the lapilli were made to the nearest micron.

Results

Larval herring growth

Otoliths were dissected, mounted, and analyzed for a combined total of 1,746 larval herring. Growth with

Table 1

Cruise information for larval Atlantic herring, *Clupea harengus*, specimens collected for otolith analysis during the autumn–winter field season in the Nantucket Shoals–Georges Bank region.

Vessel	Cruise no.	No. of sta.	Cruise sampling dates	No. of larvae	Mean length (mm)	Mean age (d)
1976–77						
Wieczno	76–03	1	14 Oct–03 Nov	18	16.9	31.1
Researcher	76–01	5	27 Nov–11 Dec	90	21.5	52.0
Mt. Mitchell	77–01	4	13 Feb–24 Feb	48	30.3	131.1
Anton Dohrn	77–01	1	15 Mar–21 Mar	34	31.8	148.4
1988–89						
Delaware II	88–12	4	31 Oct–11 Nov	43	14.4	27.3
Albatross IV	88–11	5	29 Nov–10 Dec	34	21.8	44.5
Delaware II	89–01	11	05 Jan–20 Jan	77	25.4	63.2
1989–90						
Delaware II	89–07	6	06 Nov–16 Nov	117	17.3	31.5
Delaware II	89–09	9	27 Nov–16 Dec	159	23.4	50.5
Delaware II	90–01	6	04 Jan–17 Jan	106	28.0	74.8
1990–91						
Delaware II	90–12	15	30 Oct–08 Nov	112	15.9	30.9
Delaware II	90–14	18	29 Nov–14 Dec	102	22.2	48.8
Delaware II	91–01	16	04 Jan–16 Jan	100	24.3	60.7
Delaware II	91–03	5	17 Feb–22 Feb	100	29.7	89.1
1991–92						
Delaware II	91–11	15	04 Nov–14 Nov	87	13.5	27.1
Delaware II	91–13	14	04 Dec–13 Dec	85	24.8	53.9
Delaware II	92–01	10	06 Jan–13 Jan	96	25.8	65.5
Delaware II	92–02	12	29 Jan–12 Feb	96	28.6	81.2
1992–93						
Delaware II	92–12	9	26 Oct–04 Nov	74	14.1	31.0
Delaware II	92–14	5	01 Dec–18 Dec	50	24.9	59.0
Delaware II	93–01	6	05 Jan–21 Jan	101	27.7	80.5
1993–94						
Delaware II	93–12	5	02 Nov–10 Nov	50	17.0	31.7
Delaware II	93–14	6	30 Nov–10 Dec	50	22.1	46.9
Delaware II	94–01	4	06 Jan–18 Jan	50	27.7	68.6

respect to length for each of the seven field seasons studied was best described by a Gompertz-type curve. The methodology for fitting the curve is discussed in Pennington (1979). Previous uses of the Gompertz growth curve are presented in Al-hossaini et al. (1989) and Jearld et al. (1993). The Gompertz curve not only permits the calculation of growth rate but also provides mean hatching size (length at age 0) and predicted length at metamorphosis (the asymptotic limit of mean larval growth).

Analysis of the seven field seasons resulted in the following relationships, where L = standard length in mm and *Age* = number of days (increments plus 19) from hatch:

$$1976/77\ L = 33.5381e^{-1.1055e^{-0.0197Age}} \quad [n=187,\ r^2=0.8965];$$

$$1988/89\ L = 38.9217e^{-1.5483e^{-0.0213Age}} \quad [n=139,\ r^2=0.8951];$$

$$1989/90\ L = 35.2189e^{-1.6232e^{-0.0271Age}} \quad [n=379,\ r^2=0.8914];$$

$$1990/91\ L = 36.0859e^{-1.6104e^{-0.0240Age}} \quad [n=382,\ r^2=0.9161];$$

$$1991/92\ L = 34.1978e^{-1.9677e^{-0.0320Age}} \quad [n=313,\ r^2=0.8540];$$

$$1992/93\ L = 34.1176e^{-2.1559e^{-0.0312Age}} \quad [n=204,\ r^2=0.9085];$$

$$1993/94\ L = 37.4796e^{-1.8986e^{-0.0276Age}} \quad [n=142,\ r^2=0.9435].$$

A summary of the growth parameters generated by the above equations may be found in Table 2. Plots of the Gompertz curves fitted to standard length vs. age in days are presented in Figure 2.

In order to compare the rate of growth for the seven seasons, the Gompertz curves were linearized and examined for homogeneity of slope with t-tests (Table 3; Fig. 3). With this method, three groupings were discernible: 1) the 1976–77 season; 2) the 1988–89, 1989–90, and 1990–91 seasons; and 3) the 1991–92, 1992–93, and 1993–94 seasons. Larval growth for the 1976–77 season was the slowest (0.16 mm/d) of the time series, and although larvae for this season had the greatest hatch length, standard length at 120 days posthatch was 2.2 to 4.8 mm less than that in the other six years. There was no significant difference at the 0.05 level between the 1988–89, 1989–90, and 1990–91 seasons. Hatching length for these three seasons differed by less than 1.5 mm, and overall rates of growth for the first 120 days were identical. The rate of growth during the overwintering period of 1988–89 was the greatest of the seven years and compensated for the relatively slow growth earlier in the season. Larvae were on average 2.7 mm smaller at hatching in the autumns of 1991, 1992, and 1993 than in the preceding three years. The rate of growth for the first 40 to 60 days was considerably faster than that in previous years; however, this initial rapid increase in length was followed in 1991–92 and 1992–93 by a period of slower than average growth. The overall higher rates of growth in these two years were not enough to compensate for the small size of larvae at hatching (4.0–4.8 mm), and projected lengths at metamorphosis (34.1–34.2 mm) were smaller than in all previous years except 1976–77. Although hatching lengths in 1993–94 were small, growth was good throughout the season, and the average length at 120 days posthatch (35.0 mm) was the largest of the time series.

Predictability

A generalized growth model for larval herring was created by pooling data (n=1,559) from the six most recent field seasons (1988–94) and by fitting them with a Gompertz curve:

$$L = 34.9959e^{-1.7424e^{-0.0281Age}} \quad [r^2=0.8863].$$

The model tracks growth for the first four months of life from an estimated hatch length of 6.1 mm to a predicted length at 120 days posthatch of 33.0 mm (0.22 mm/d). Figure 4 shows the growth curve with 95% confidence intervals for predicting standard length (mm) for a given age in days. This information is also presented in Table 4 along with age-specific growth rates.

Because it is desirable, especially during field surveys when direct analysis of otoliths is impossible, to be able to estimate the age of larvae based on their length, inverse regression (Draper and Smith, 1966) was performed on the Atlantic herring composite growth curve to establish confidence intervals for predicting age from a given standard length. In its reduced form the equation obtained for herring was

$$\begin{matrix} X_U \\ ] \\ X_L \end{matrix} = \frac{\ln\left(\dfrac{1-X_0 \pm 0.0470t}{\left(\left((X_0-0.7523)^2/26.5957\right)+(1+1/n)\right)^{1/2}}\right)}{-0.0281}$$

where X_U and X_L = upper and lower confidence limits;
X_0 = $1-e^{-0.0281}$; and
n = sample size.

Table 2

Summary of larval Atlantic herring growth parameters based on otolith anaylsis for the autumn–winter field seasons of 1976–77, 1988–89, 1989–90, 1990–91, 1991–92, 1992–93, and 1993–94.

	1976	1988	1989	1990	1991	1992	1993
Sample size	187	139	379	382	313	204	142
Corrected standard length (mm)							
Hatching length	11.1	8.3	6.9	7.2	4.8	4.0	5.6
Inflection of lapillus	—	—	29.1	29.1	28.9	29.4	—
120 days posthatch	30.1	34.5	33.1	33.0	32.9	32.4	35.0
Metamorphosis length	33.5	38.9	35.2	36.1	34.2	34.1	37.5
Growth rate (mm/d)							
Age (d)							
0	0.24	0.27	0.31	0.28	0.30	0.26	0.29
20	0.23	0.30	0.35	0.32	0.41	0.39	0.38
40	0.20	0.28	0.30	0.29	0.35	0.36	0.35
60	0.16	0.23	0.22	0.23	0.23	0.26	0.26
80	0.12	0.18	0.15	0.16	0.14	0.16	0.18
100	0.09	0.13	0.09	0.11	0.08	0.09	0.11
120	0.06	0.09	0.06	0.07	0.04	0.05	0.07
Overall	0.16	0.22	0.22	0.22	0.23	0.24	0.24

Table 3

Summary statistic comparing growth curves for the seven field seasons analyzed. Values in boldface indicate no significant difference at the 5% level.

	t-value						
	1976–77	1988–89	1989–90	1990–91	1991–92	1992–93	1993–94
1976–77	—						
1988–89	–5.9188	—					
1989–90	–10.4849	**–1.7146**	—				
1990–91	–10.6624	**–1.3390**	**–0.6648**	—			
1991–92	–15.0114	–6.4908	–6.6106	–7.5418	—		
1992–93	–17.5134	–8.5801	–9.5920	–10.7229	–2.7409	—	
1993–94	–13.5369	–5.4810	–4.9987	–5.8684	**0.9600**	–3.5349	—

Table 5 provides predicted ages of Atlantic herring for given standard lengths with 70% and 95% confidence limits, and Figure 5 shows the fitted growth curve bracketed by its confidence limits.

Otolith growth

Because past studies have demonstrated a strong relationship between mean otolith diameter (μm) and age (d) (Bolz and Lough, 1987), sagittal growth for the seven seasons was analyzed and compared. The extremely slow growth in otolith diameter during the 1976–77 season was dramatically different from the other six years and resulted in a one-third smaller diameter at metamorphosis (Fig. 6). During 1988–89 and 1993–94, there appeared to be a decoupling of somatic and otolith growth, such that 120-day-old larvae were approximately 1.4–2.6 mm longer than those in the four other recent field seasons and had a smaller otolith diameter.

Beginning with the 1989–90 season, the length of the lapilli, as well as that of the sagittae, was measured. A plot of diameter of the lapillus versus age in days showed an abrupt increase in its rate of growth at approximately 2.5 months of age (Fig. 7). In 1989–90 and 1990–91 the point of flexion occurred at a length of 29.1 mm SL when the larvae were 79 and 84 days old, respectively. Change in the growth of

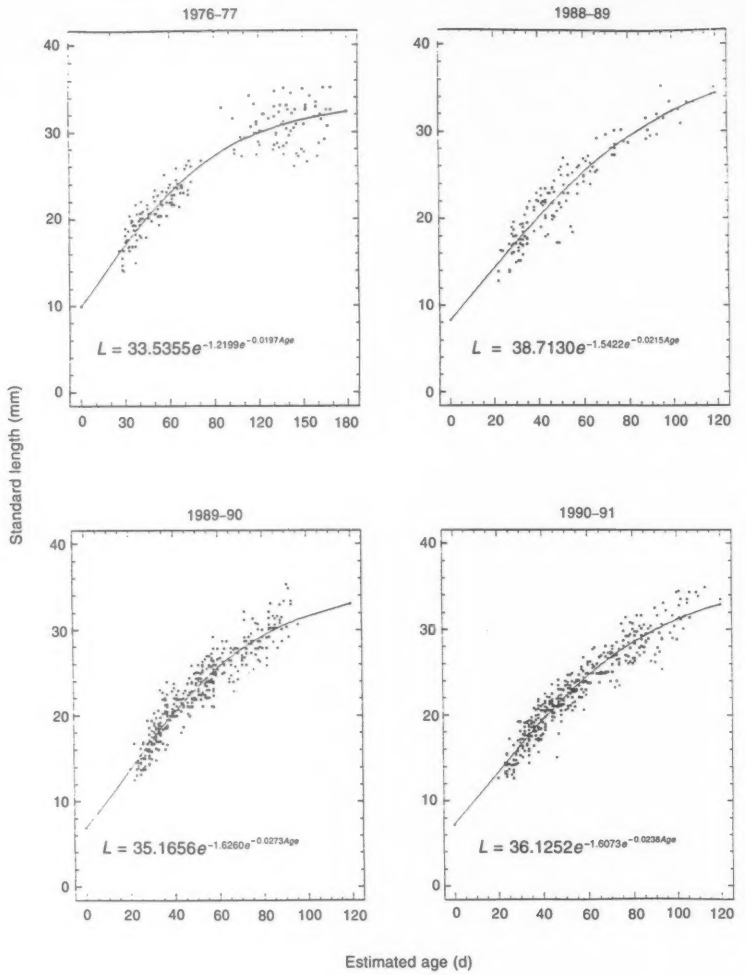

Figure 2

Gompertz growth curves and equations fitted to plots of standard length and estimated age in days (number of otolith increments plus 19) for larval Atlantic herring collected in the Nantucket Shoals–Georges Bank region during the autumn–winter field season.

the lapillus occurred at 77 days in 1991–92 and at 86 days in 1992–93 when the fish were respectively 28.9 and 29.4 mm SL. Owing to the small number of larger individuals sampled during the 1993–94 season, it was not feasible to determine when inflection took place.

Discussion

With the collapse of the herring fishery in the Nantucket Shoals–Georges Bank region during the autumn of 1976, initial larval abundance dropped from an estimated 62.5×10^{12} larvae in 1975 to 2.8×10^{12} in 1976 (Lough et al., 1985). This low abundance was further diminished by strong and persistent northerly winds that occurred during November, January, and February of the 1976–77 season (Wright, 1979; Bolz and Lough, 1984). The computed Ekman transport indices (Lough et al., 1979) are indicative of strong southerly transport. These winds with their resultant offshore surface drift would have disrupted the normal spatial distribution of prey (Maillet and Checkley, 1991).

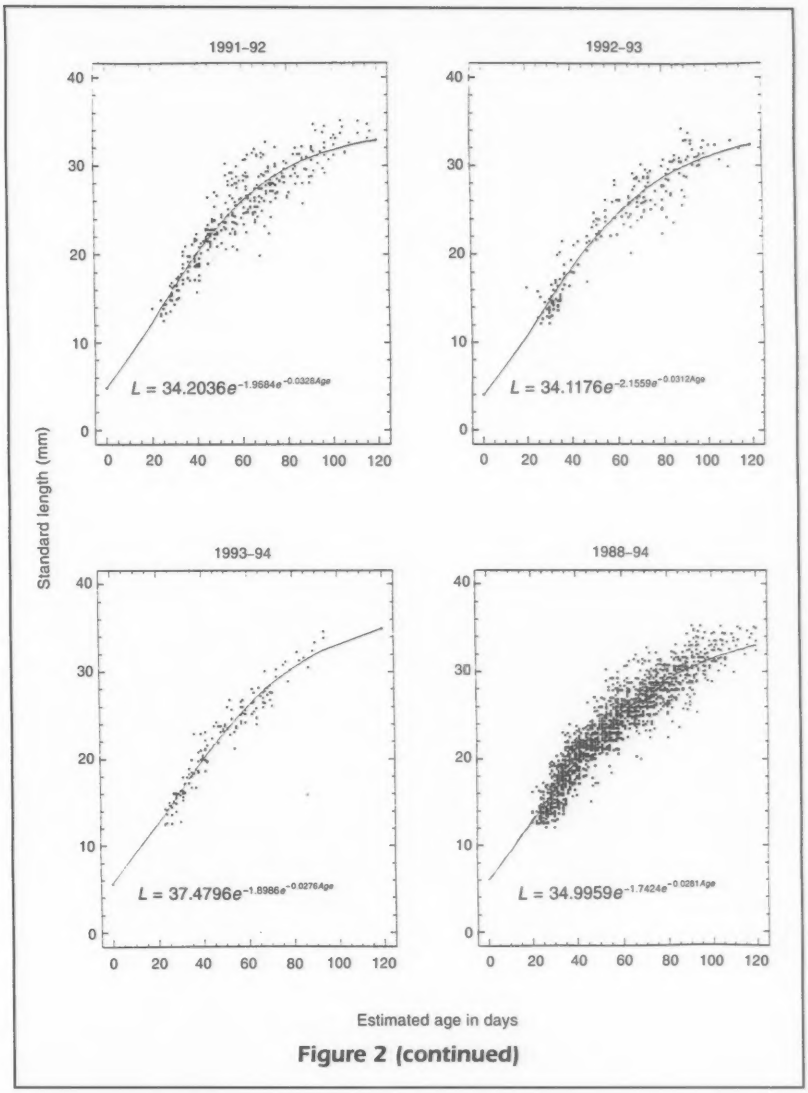

Figure 2 (continued)

Fish hatched in 1976 were longer by 2.8 to 7.1 mm SL than those collected during the 1980's and early 1990's. Since temperatures in the autumn of 1976 did not differ significantly from the long-term average (Mountain and Holzwarth, 1989), a density-dependent function is the most likely explanation for this difference. It is possible that the less dense beds enhanced growth by permitting eggs to be oxygenated better or that the diminished spawning population produced eggs with greater food reserves (Blaxter and Hunter, 1982). Despite their initially robust appearance, larvae during the 1976–77 season exhibited poor growth and high mortality (Lough et al., 1979). The severe storms discussed above most likely dispersed the prey of larval herring and led to a reduction in daily food rations. Poor feeding is reflected in the rapid lessening of mean otolith diameter noted during 1976–77. This observation is in agreement with the previous study of Cohen and Lough (1983), where larvae collected during the 1976 season had lower prey numbers and biomass per larva than those in 1974 and 1975. Similar results were found by Karakiri et al. (1989) in their study of age-0 plaice (*Pleuronectes platessa* L.). They also concluded that food limitation accounted for an observed difference in growth between two years with similar

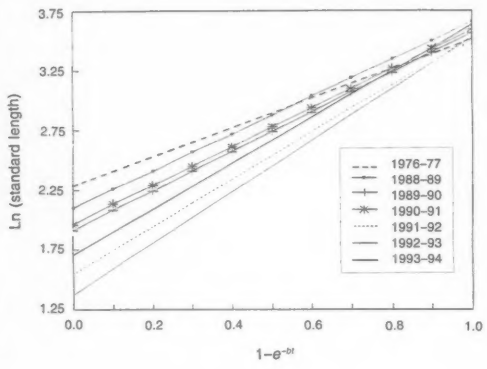

Figure 3

Comparison of the regression lines for the seven field seasons analyzed (b = rate of exponential decay; t = age in days).

temperature regimes and that the difference was likewise reflected in daily otolith increment widths.

Several studies have observed a poor correlation between otolith length and fish length (Secor et al., 1989; Moksness and Wespestad, 1989), and this was partly the case in the present work. Since increments may continue to be deposited during periods of slow or negative somatic growth, caution must be exercised in estimating age based solely on length relationships. After 120 days of growth, the fish in the 1988–89 and 1993–94 seasons showed smaller mean otolith diameters than did fish in 1989–90, 1990–91, 1991–92, and 1992–93 seasons, despite their having larger mean standard lengths. There is, however, a strong relationship between mean otolith increment width and the somatic rate of growth as expressed in mm/d of SL. From 60 to 120 days of age, larval herring grew very slowly in 1976–77 and exhibited thin increments; whereas in 1988–89, growth was more rapid and the increments were wider. Secor et al. (1989) found evidence of a lag effect between food ration and its reflection in the otoliths and, until this finding can be demonstrated in herring, it is perhaps best to cite trends rather than attempt to relate a given increment to a specific event.

The predictive model for Atlantic herring growth presented above has to be viewed as general in nature, and the widening of the confidence intervals with increasing length (Tables 4 and 5; Figs. 4 and 5) must be kept in mind. Natural variability of length at age and difficulty in the reading of otoliths increase as fish become older and make precise age determinations extremely difficult. For example, the ability to predict correctly the age of an individual herring larva at the 70% confidence level decreases from ±2 days at 8 mm SL to ±2 weeks at 30 mm. In spite of this problem, otolith ageing of field-caught larvae provides a degree of precision not possible with indirect methods based on size-frequency analysis (Ebert, 1973).

The inflection noted in the rate of otolith growth (Fig. 7) occurs at an age when the otic bullae would

Table 4

Mean standard length at age, 95% prediction limits, and growth rate of larval Atlantic herring from hatch through 120 days, estimated from the Gompertz growth model fit.

Age (d)	Mean length (mm)	95% prediction limits		Growth rate (mm/day)
		Lower	Upper	
0	6.1	5.1	7.1	0.30
10	9.2	7.9	10.9	0.35
20	12.8	10.9	15.1	0.36
30	16.4	13.9	19.3	0.35
40	19.7	16.8	23.2	0.32
50	22.7	19.3	26.7	0.28
60	25.3	21.5	29.7	0.23
70	27.4	23.3	32.2	0.19
80	29.4	24.7	34.2	0.15
90	30.4	25.9	35.8	0.12
100	31.5	26.8	37.1	0.09
110	32.3	27.5	38.1	0.07
120	33.0	28.0	38.8	0.06

Table 5

Predicted age in days, with 70% and 95% prediction limits, of larval Atlantic herring for a given standard length.

Observed standard length (mm)	Predicted age (d)	70% prediction limits		95% prediction limits	
		Lower	Upper	Lower	Upper
6.1	0	—	1.7	—	3.2
8.0	5.9	3.9	7.9	2.2	9.6
10.0	11.7	9.4	14.0	7.4	16.0
12.0	17.3	14.6	20.0	12.3	22.3
14.0	22.8	19.6	26.0	17.1	28.5
16.0	28.4	24.7	32.1	21.8	35.0
18.0	34.2	29.9	38.5	26.5	41.9
20.0	40.3	35.3	45.3	31.3	48.3
22.0	46.9	41.0	52.8	36.4	57.4
24.0	54.3	47.1	61.5	41.7	66.9
26.0	62.8	53.9	71.7	47.5	78.1
28.0	72.9	61.5	84.3	53.7	92.1
30.0	86.0	70.5	101.5	60.7	111.3

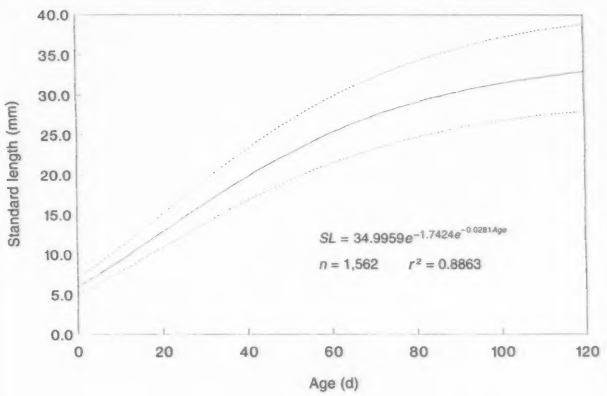

Figure 4

Gompertz growth curve for larval Atlantic herring with 95% confidence intervals for predicting standard length (mm) for a given age in days.

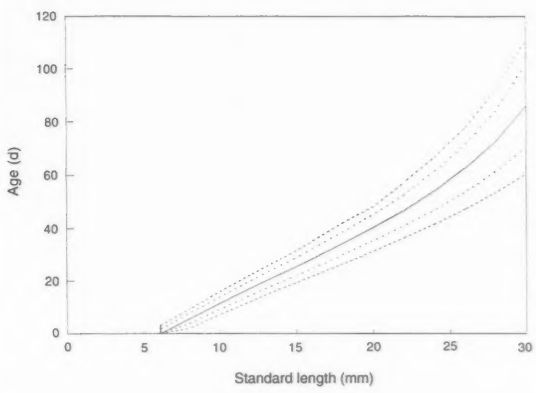

Figure 5

Inverse regression of Atlantic herring growth curve with 70% and 95% confidence intervals for predicting age in days for a given standard length (mm).

be expected to fill with air. Enlargement at this time of the lapilli and, less dramatically, of the sagittae and maculae would allow larvae to take greater advantage of the wave amplification conferred by a full air bladder and bullae. In order to successfully avoid predation and to control vertical migration, this should occur at as early an age as possible. Analysis of otolith growth is probably the only way to estimate the timing of this developmental landmark in field-caught larvae. Knowing when this occurs may permit a better understanding of population anomalies. The necessary morphometric data are lacking for the 1976–77 season; however, from the analysis of recent seasons, the storm events in late November 1976 would be expected to have occurred while many of the larvae were at this critical life stage. This co-occurrence of storm events and critical life-stage events would have caused additional mortality to an already stressed population.

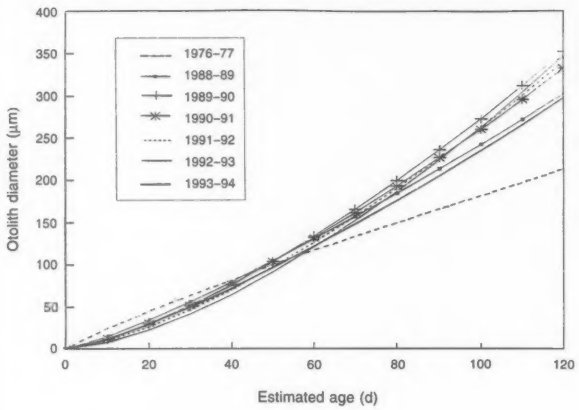

Figure 6

Comparison of changes in otolith growth for larval herring during the autumn-winter period of the seven years in the study.

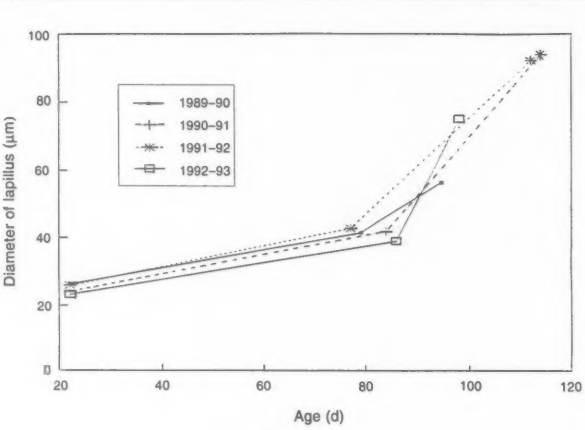

Figure 7

Growth of larval herring lapillus showing increase in rate of growth at approximately 2.5 months of age.

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Estimated paralarval drift and inferred hatching sites for *Ommastrephes bartramii* (Cephalopoda: Ommastrephidae) near the Hawaiian Archipelago

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Abstract.—Research was conducted to test the hypothesis that spawning of the oceanic squid *Ommastrephes bartramii* in the central North Pacific is related to the proximity of the Hawaiian Archipelago. Paralarvae were collected during five plankton surveys near the Hawaiian Island chain during the 1991–93 spawning seasons. In total, 1,720 *O. bartramii* paralarvae were collected from 406 tows. Estimation of ages and hatch dates of all squid was inferred from analysis of statolith microstructures from 85 specimens. A well-defined relationship existed between the number of statolith growth increments and the dorsal mantle length of the paralarvae. Estimated hatch dates of individuals collected during the three years surveyed ranged between mid-January and early April. Spawning sites were then estimated from hatch dates by backcalculating with physical data on the speed of ocean currents near the archipelago. Although estimated spawning of *O. bartramii* did often occur along the island chain, spawning was not limited to nearshore waters. Some animals hatched, on the basis of estimated current speeds, at least 646 kilometers away from the archipelago. Projected hatching locations of more than 72% of all collected paralarvae were at least 10 kilometers from shore. Data do not support the hypothesis that the location of the spawning grounds in this region is solely related to the position of the Hawaiian Archipelago.

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The neon flying squid, *Ommastrephes bartramii* (Lesueur), is an oceanic species occurring worldwide in subtropical and temperate waters (Roper et al., 1984). In the North Pacific, *O. bartramii* paralarvae have been collected from several areas: from January through May, paralarvae are found southeast of Honshu Island, Japan (Okutani, 1968, 1969; Saito and Kubodera, 1993); and during May, paralarvae are found along 25–26°N latitude between 143–166°E longitude, and along 29°N latitude between 161–160°E longitude (Hayase, 1995). Paralarvae also occur near the Hawaiian Archipelago from February to May (Young and Hirota, 1990; Hayase, 1995; Bower et al.[1]; Hayase[2]). A study of paralarvae collected near the Hawaiian Archipelago during 1991–93 found no systematic relationship between the distribution and abundance of *O. bartramii* paralarvae and distance from the archipelago (Bower et al.[1]). This study, however, did not account for the effects of age and paralarval drift on the distribution patterns found. The present study attempts to identify more clearly possible spawning areas by considering these factors.

Statoliths from teuthoid squids commonly contain growth increments that can be used for age determination. After conducting a detailed age analysis of *Loligo opalescens*, Spratt (1978) argued that some increments in the statolith were deposited daily, as in fish otoliths. Since then, a number of studies have been conducted to determine the frequency of increment formation (Dawe et al. [1985] on *Illex illecebrosus*; Hurley et al. [1985] on *I. illecebrosus*; Lipinski [1986] on *Alloteuthis subulata*; Jackson [1989, 1990]; and Nakamura and Sakurai [1991] on *Todarodes pacificus*; also see reviews by Rodhouse and Hatfield [1990] and Jackson [1994]). The data provide strong support for the hypothesis that growth increments form at the rate of one per day in both loliginid and ommastrephid squids. Although validation of the growth increments of *O. bartramii* has not been accomplished, I have assumed that they form daily for this study.

[1] Bower, J. R., R. E. Young, J. Hirota, P. Flament, M. Seki, and K. Bigelow. 1996. Distribution and abundance of cephalopod paralarvae near the Hawaiian Archipelago. In prep.

[2] Hayase, S. 1989. Cruise report of flying squid spawning survey by the *Hokuho Maru* in the North Pacific in April–May 1989, 21 p. Document submitted to the Annual Meeting of the International North Pacific Fisheries Commission, Seattle, Washington, 1989 October.

Vertical distribution data suggest that *O. bartramii* paralarvae occur within the 0–40 m depth layer during both day and night (Okutani, 1968; Young and Hirota, 1990). Upon hatching, paralarvae are active swimmers, but owing to their small size remain planktonic for an unknown period, presumably for several weeks. Given the role of ocean currents in the transport of cephalopod paralarvae, any analysis of cephalopod paralarval distribution requires an investigation of the prevailing oceanographic currents to determine from what region the animals have been advected since hatching. Although there are few records of naturally spawned eggs or egg masses from oceanic cephalopods and no observations of *O. bartramii* egg masses, O'Dor and Balch (1985) have suggested that pelagically spawned egg masses may become suspended in the mesopelagic zone, where reduced current speeds would limit transport of egg masses away from spawning sites. I have assumed that each paralarva hatched at the site at which it was spawned.

Korzun et al. (1979) have suggested that spawning locations of *O. bartramii* may be related to the position of islands. The present study was undertaken to determine whether and how the spawning locations of *O. bartramii* from the North Pacific are related to the proximity of the Hawaiian Archipelago. This objective was addressed by examining the distribution and ages of paralarvae captured during five plankton surveys near the Hawaiian Island chain from 1991 to 1993 with ocean current data derived from Lagrangian tracers and by estimating geostrophic flow.

Materials and methods

Collection and ageing of paralarvae

Five plankton surveys were conducted near the Hawaiian Archipelago to collect cephalopod paralarvae (Fig. 1). Plankton samples were collected during 6–15 February 1991, 5–26 February 1992, and 4–19 February 1993 with the Hokkaido University (Japan) ship FTS *Hokusei Maru*, and during 5–20 February 1991 and 22 March–7 April 1992 with the RV *Townsend Cromwell* of the National Marine Fisheries Service (NMFS). The standard sampling procedure during all surveys was to conduct 30-minute oblique tows to 100 m depth.

The *Hokusei Maru* February 1991 (*HM*-Feb 91) survey sampled paralarvae at seven stations along an inshore–offshore transect to the northeast of the Hawaiian Island chain from Kauai Island (Kauai transect), including a lone station in the lee of Hawaii Island. Windward stations were positioned 9, 16, 106, 235, 349, 460, and 583 kilometers offshore. Thirty-six tows (mean depth=95 m; SD=9 m) were taken. Sampling consisted of five back-to-back replicate tows at each station. This and subsequent *Hokusei Maru* surveys used a 4-m^2 ring net equipped with 0.505-mm mesh, a General Oceanics flowmeter, and a Benthos time-depth recorder.

The *Townsend Cromwell* February 1991 (*TC*-Feb 91) survey sampled at ten stations along the archipelago. Transects orthogonal to the archipelago were

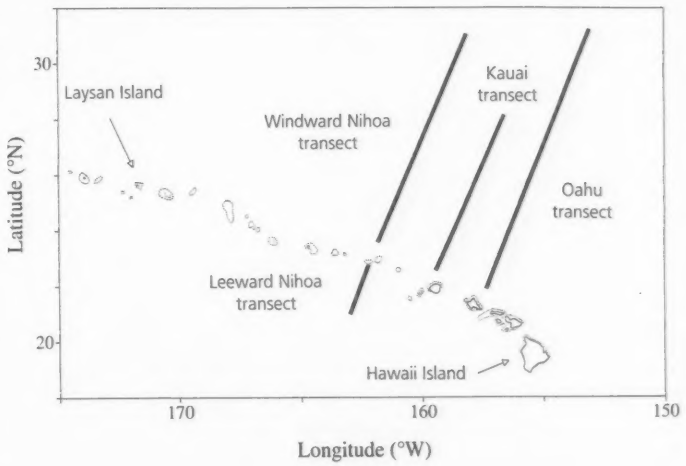

Figure 1

Map of the Hawaiian Archipelago showing the study area and transects surveyed during the five cruises.

abandoned because of inclement weather north of the ridge, restricting most sampling to nearshore waters. Stations were located 13, 14, 15, 16, 25, 28, 28, 207, 228, and 232 kilometers offshore. Forty-four tows were conducted in a stepped oblique fashion (mean depth=93 m; SD=12 m). Sampling consisted of between one and seven back-to-back replicate tows at each station with a 4-m^2 ring net equipped with 0.505-mm mesh.

During the *Hokusei Maru* February 1992 (*HM*-92) survey, paralarvae were collected along the windward Nihoa and Kauai transects, including three stations southwest of the archipelago along the leeward Nihoa transect and a lone station in the lee of Oahu Island. The Kauai transect included stations sampled during the *HM*-91 survey. One hundred thirty-one tows were collected at sixteen sampling stations (mean depth=70 m; SD=14 m). Owing to high variability in the catch rates from the *HM*-91 survey, the number of tows taken at each sampling station was increased from five to between seven and ten back-to-back replicate tows. Stations along the Kauai transect were located 11, 41, 142, 235, 337, 471, 585, and 713 kilometers offshore. Nihoa transect stations were located 26, 181, and 269 kilometers windward, and 25, 126, and 256 kilometers leeward of the archipelago. Four scheduled stations along the windward Nihoa transect were canceled because of inclement weather.

During the RV *Townsend Cromwell* March–April 1992 (*TC*-92) survey, four to eight replicate tows were conducted at fourteen stations along the windward Nihoa and Oahu transects. One hundred tows (96 with a 2-m^2 ring; 4 with a 4-m^2 ring) were conducted in a stepped oblique fashion (mean depth=94 m; SD=13 m). The net carried a Wildlife Computers time-depth recorder. Stations were located between 52 and 1,161 kilometers offshore.

During the *Hokusei Maru* February 1993 (*HM*-93) survey, paralarvae were collected along the same two transects, northeast of the Hawaiian Island chain, that had been sampled in February 1992, including three stations southwest of the archipelago (leeward Nihoa transect) and a lone nearshore test station (only two tows conducted) northeast of Oahu Island. Ninety-five tows (mean depth=92 m; SD=23 m) were collected at twelve sampling stations. Seven to ten back-to-back replicate tows were taken at each station.

Specimens from the *Hokusei Maru* surveys were fixed in 4% formalin and preserved in 50% isopropyl alcohol within 3–6 hours to prevent possible acidic degradation of the calcareous statoliths. *TC*-91 survey samples were fixed in 10% formalin and preserved in 50% isopropyl alcohol. *TC*-92 survey samples were fixed in 6% formalin and preserved in 50% isopropyl alcohol. Statoliths from specimens stored in formalin longer than six hours darkened and proved unreadable.

Paralarvae of the family Ommastrephidae were identified to genus and species level according to figures and descriptions of Hawaiian ommastrephids published by Young and Hirota (1990) and Harman and Young (1985). The dorsal mantle length of each *O. bartramii* paralarva was measured to the nearest 0.1 mm with an ocular micrometer in a stereomicroscope.

Statoliths were removed from the paralarvae with fine dissecting forceps under a stereomicroscope. First, the paralarval funnel was removed, revealing the ovate statocyst. Statoliths were clearly visible within the statocyst as paired, white, opaque structures. The excised statocyst was transferred to a microslide, where it was gently pulled apart, permitting one of the statoliths to fall onto the slide. The statocyst with the remaining statolith inside was then transferred to a separate slide where the statolith was similarly removed. Statoliths were rinsed in distilled water and air-dried before analysis. When dried, statoliths were embedded in thermal plastic by heating the plastic to 77°C.

Statoliths from 85 animals (mantle length: 1.0–4.7 mm) were used for growth increment analysis. Paralarvae used for statolith examination were collected during the *HM*-91, *HM*-92, and *TC*-92 surveys. Growth increments on *O. bartramii* statoliths consisted of two components, a broad, translucent ring and a narrow, dark ring. Using a Zeiss compound microscope (400×), increments were counted from the nucleus to the outer margin of the dorsal end of the lateral dome. Examinations were made with transmitted light. Counts of each statolith were conducted on three separate occasions and averaged for a mean increment value. Increments in the outermost portion of the lateral dome and the innermost portion near the nucleus could not be counted in some cases; therefore the number of increments on those portions was estimated by extrapolation.

Data treatment

Age for each of the 85 paralarvae used for growth increment analysis was determined from the mean of the three counts of statolith growth increments. The exponential equation $y=ae^{bx}$ was fitted to the data for the mantle-length–increment-count relationship. Age estimates of all other paralarvae were based on this relationship curve.

Estimated ocean current speeds and directions

Patterns of ocean currents near the Hawaiian Archipelago were defined by the trajectories of near-

surface drifters and by dynamic height measurements from conductivity-temperature-depth (CTD) probes. Four ARGOS-tracked drifters released by the National Marine Fisheries Service were used as Lagrangian tracers of the surface currents during the 1992 survey periods to assess "typical" current speeds and directions near the Hawaiian Archipelago. Drifter positions were recorded every six hours over the survey period. Each drifter's Lagrangian net path was plotted. Geostrophic flow measurements were calculated between each pair of successive sampling stations during the three *Hokusei Maru* surveys on the basis of dynamic height measurements taken at each sampling station from CTD casts to 1,200 m. Sampling stations averaged approximately 110 km and 24 hours apart.

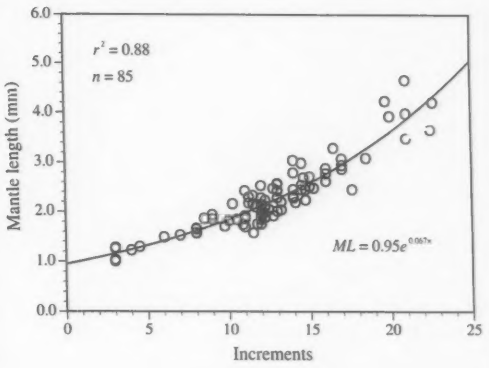

Figure 2

Relationship between paralarval mantle length and number of daily growth increments in statoliths of *Ommastrephes bartramii*, and proposed growth curve.

Results

A total of 1,720 *O. bartramii* paralarvae was collected at 41 of the 59 sampling stations, making up 16.5% of the cephalopod paralarvae caught. Sizes of *O. bartramii* ranged from 0.9 mm to 8.3 mm ML.

Age–mantle-length relationship

Statolith growth increment counts ranged from 3 to 22.7 (Table 1). A well-defined relationship existed between the number of statolith growth increments and the dorsal mantle length of the paralarvae, with the exponential function yielding a good fit for the regression (r^2=0.88) of the number of increments on the dorsal mantle length (Fig. 2). The following exponential model was fitted to the data:

$$ML = 0.95e^{(0.067x)},$$

where ML is the dorsal mantle length in millimeters and x equals the number of increments. This equation was used to estimate the ages (x) of the 1,635 paralarvae not examined during statolith increment analysis. The y-intercept of the exponential function (a=0.95 mm) is close to the actual hatching length (ca. 1 mm).

Size structure, ages, and projected hatch dates

The dorsal mantle length ranges of *O. bartramii* paralarvae varied slightly among surveys (Fig. 3). The largest range of size occurred during the *TC*-91 survey (0.9–8.3 mm), and the smallest range of size occurred during the *HM*-91 survey (1.0–5.6 mm).

Estimates of paralarval ages for total samples, predicted from the exponential mantle length on age model, ranged from 1 to 30 days. Projected paralarvae hatch dates for the five surveys are summarized in Figure 4. During the *HM*-91 and *TC*-91 surveys, captured paralarvae were estimated to have hatched between 13 January and 8 February. During the *HM*-92 and *TC*-92 surveys, estimated hatch dates of captured paralarvae fell between 22 January and 1 April. During the *HM*-93 survey, estimated hatch dates of captured paralarvae fell between 11 January and 6 February.

Paralarval size with distance offshore

Mean mantle lengths at each station were compared with distance from the archipelago (Fig. 5). The mean mantle lengths at each station were not significantly correlated (P>0.05; Student's t-test) with distance offshore for any of the five surveys.

Hydrographic observations

No clear advective current patterns could be estimated from the ARGOS-tracked drifters' tracks (Fig. 6). Average net displacement of the four drifters near the Hawaiian Archipelago was 2.5 km per day. During the *HM*-91 survey, CTD data revealed surface to 50-m flows ranging from 4.1 to 16.0 cm per second relative to 1,000 m in reversing bands relative to the archipelago north of the island chain. During the *HM*-92 survey, CTD data revealed flows ranging from 0.0 to 13.8 cm per second relative to 1,000 m in reversing bands relative to the archipelago both north and south of the island chain; *HM*-93 CTD data revealed

flows ranging from 1.6 to 23.6 cm per second relative to 1,000 m in reversing bands both north and south of the island chain.

In summary, mean current speeds near the Hawaiian Archipelago range between 0.30 and 0.42 knots for geostrophic flow normal to the transects and about 0.06 knots for ARGOS-drifter–measured displacement, with flow near the islands complex and highly variable. The drifter data are considered to be the more reliable estimate of mean-surface drift.

Projected spawning grounds

An average current speed (2.5 km per day) estimated from the four drifters tracked in the region was used together with age estimates to infer possible areas of spawning for *O. bartramii*. To determine whether paralarvae captured at some distance from the archipelago could have been carried to their position by currents from a spawning site next to the archipelago, a "best-case" scenario was used that assumed

Table 1

Size frequency of *Ommastrephes bartramii* paralarvae for 85 statoliths examined with statolith mean increment count, standard deviation (SD), and increment count range for each dorsal mantle length (DML). Specimens were collected from *Hokusei Maru* February 1991, *Hokusei Maru* February 1992, and *Townsend Cromwell* March–April 1992 surveys.

				Count range		
DML (mm)	*n*	Count mean	SD	min	max	range
1.0	2	3.0	0.0	3.0	3.0	0
1.1	0					
1.2	1	4.0	—	—	—	—
1.3	3	3.5	0.9	3.0	4.5	1.5
1.4	0					
1.5	2	6.5	0.7	6.0	7.0	1.0
1.6	4	8.9	1.8	8.0	11.5	3.5
1.7	4	9.9	1.4	8.0	11.0	3.0
1.8	4	11.1	1.0	10.0	12.0	2.0
1.9	9	10.8	1.6	8.5	12.8	4.3
2.0	5	12.6	0.5	12.0	13.3	1.3
2.1	4	11.9	0.3	11.5	12.3	0.8
2.2	7	12.5	1.6	10.3	14.8	4.5
2.3	6	12.6	1.2	11.3	14.0	2.7
2.4	7	14.0	2.0	11	17.6	6.6
2.5	5	13.9	1.4	12	15.3	3.3
2.6	3	14.0	1.7	13	16	3.0
2.7	2	14.8	0.3	14.6	15	0.4
2.8	2	15.0	1.4	14	16	2.0
2.9	3	16.7	0.6	16	17	1.0
3.0	2	14.3	0.4	14	14.5	0.5
3.1	2	17.8	1.1	17	18.5	1.5
3.2	0					
3.3	1	16.5	—	—	—	—
3.4	0					
3.5	1	21.0	—	—	—	—
3.6	0					
3.7	1	22.5	—	—	—	—
3.8	0					
3.9	1	20.0	—	—	—	—
4.0	1	21.0	—	—	—	—
4.1	0					
4.2	2	21.2	2.1	19.8	22.7	2.9
4.3	0					
4.4	0					
4.5	0					
4.6	0					
4.7	1	21.0	—	—	—	—
Total	85					

a unidirectional flow away from the islands. Table 2 shows the estimated percentage of paralarvae taken at each sampling station that could not have been spawned within 10 km of the archipelago. The projected spawning grounds of individuals collected during the five surveys are shown in Figures 7–11.

Discussion

New information was obtained on the estimated spawning areas of the squid *Ommastrephes bartramii* with respect to the Hawaiian Archipelago over the 1991–93 winter spawning seasons. The objective of the study was to determine whether a spatial relationship exists between the Hawaiian Archipelago and *O. bartramii* spawning grounds. The results presented here suggest that although estimated spawning of *O. bartramii* did often occur along the island chain, spawning was not limited to nearshore waters; on the basis of estimated current speeds, some animals hatched at least 646 kilometers away from the archipelago. For a minimum of 72% of all paralarvae from the five surveys, projected hatching sites were located at least 10 kilometers from shore.

Statolith analysis is the most effective method for estimating age in many natural squid populations, yet preparing statoliths for counting growth increments is time-consuming, and frequently increments prove unreadable. This study showed that when a sample size is large, analysis of paralarval mantle lengths measured from a representative subsample can be used as an alternate, easier, and faster method

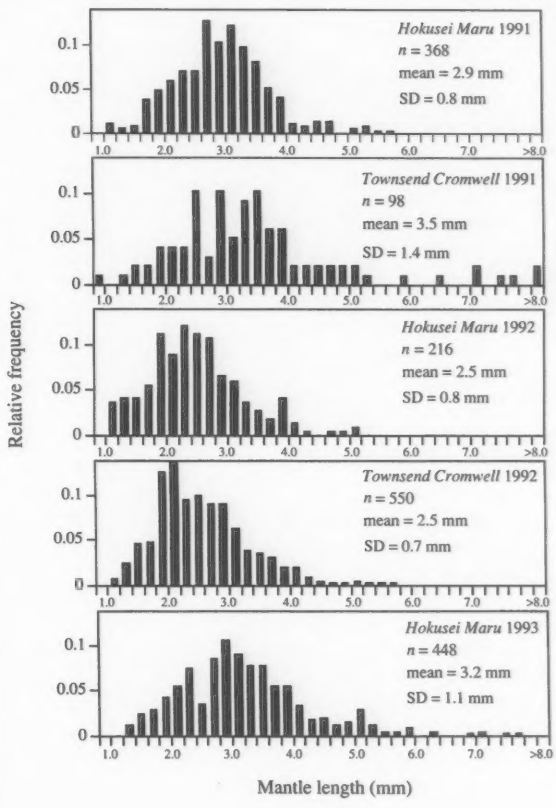

Figure 3

Size-frequency distribution of *Ommastrephes bartramii* paralarvae captured during each cruise.

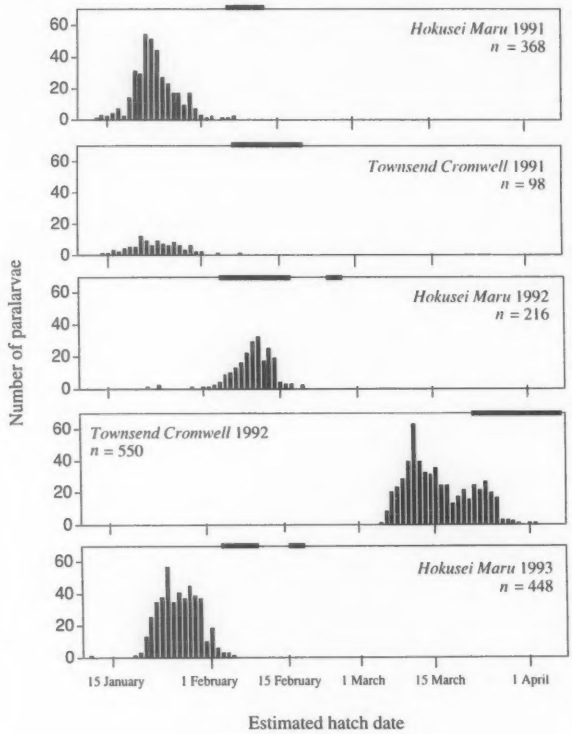

Figure 4

Frequency of projected hatch dates for *Ommastrephes bartramii* paralarvae captured during five surveys. Horizontal bars represent sampling dates.

to obtain good estimates of ages and hatch dates of *O. bartramii* paralarvae.

Growth in mantle length of *O. bartramii* paralarvae was characterized as exponential for at least 23 days after hatching. This observation agrees with that of Bigelow and Landgraf (1993), who found that growth in length of this species is exponential for at least 35 days posthatching. The growth rates of other posthatching ommastrephids have also been shown to be exponential (*Illex* sp., Balch et al., 1988; *Illex argentinus*, Arkhipkin, 1989; *Stenoteuthis oualaniensis*, Bigelow, 1991). Because growth in ommastrephids during later life tends to be linear or nearly linear, these data suggest that the overall form of growth may be approximately described as sigmoidal.

Estimated hatch dates of individuals collected during the three years surveyed ranged between mid-January and early April. Young and Hirota (1990) estimated that paralarvae caught in 1986 were spawned between late February and early April. As noted by Young and Hirota (1990), spawning may occur over a longer period, but synoptic surveys were conducted only between February and April. Surface plankton tows, conducted while the vessel drifted, and nighttime jigging at a sampling station 100 kilometers north of Oahu during March 1992, June 1992, December 1992, and April 1993, caught neither adult nor paralarval *O. bartramii* (Bower, personal observ.). More extensive nighttime jigging off the northeast coast of Oahu during mid-September–early October 1992 failed to capture adult *O. bartramii* (Bower, personal observ.). Harman and Young (1985) failed to catch *O. bartramii* paralarvae off leeward Oahu during December 1983, April 1984, August 1984, and October 1984.

Paralarvae captured over the five surveys showed a fairly broad size range of about 1–8 mm mantle

length at each station, suggesting several possible spawning scenarios. If spawning were isolated to specific geographical areas, synoptic sampling would pick up different size ranges of paralarvae, depending on the proximity of the sampling site to the spawning site. Consistently large size ranges suggest that spawning is not spatially isolated. Furthermore, they suggest that spawning by the local population does not occur in intermittent bursts but is occurring over an extended period. Estimated hatch dates confirm this. The largest squid caught was 8.3 mm, suggesting that this is approximately the size at which paralarvae are fully capable of avoiding the 4-m^2 plankton trawl or that they leave the upper 100

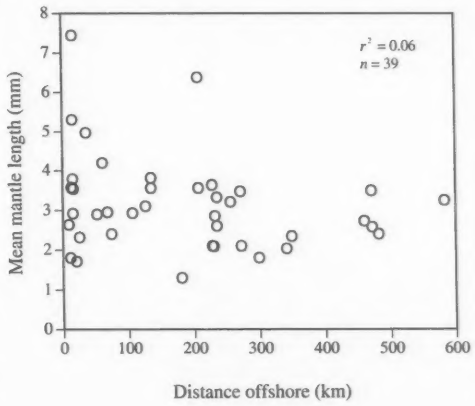

Figure 5

Relationship between mean mantle length of *Ommastrephes bartramii* paralarvae collected from each station and distance of station from land. Data from all five cruises are combined. Correlation is not significant ($P>0.05$; Student's t-test).

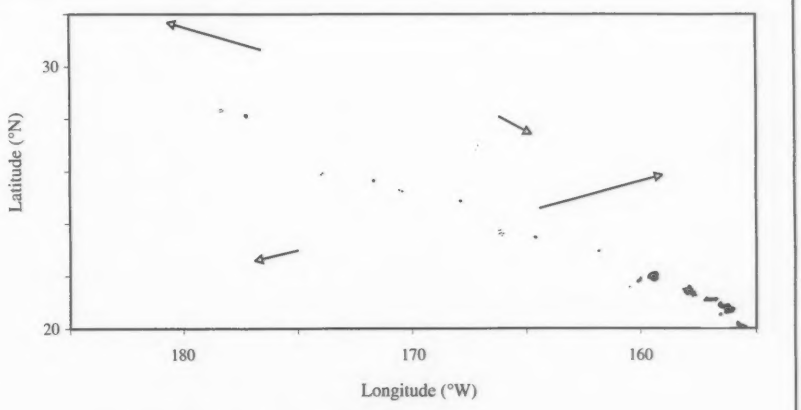

Figure 6

Net distance traveled by four ARGOS-tracked drifters near the Hawaiian Archipelago during the 1992 *Hokusei Maru and Townsend Cromwell* cruises. Time period: 22 January–1 April 1992.

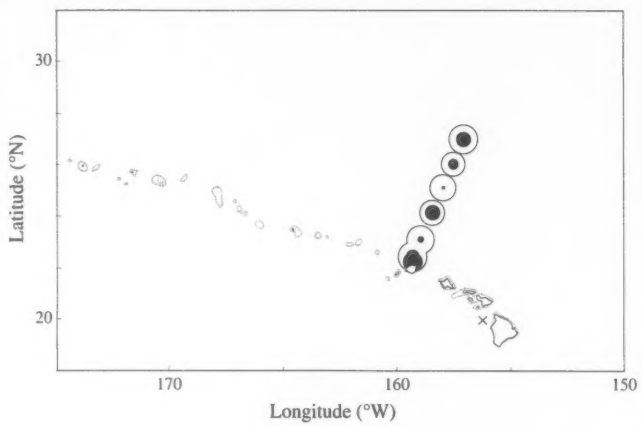

Figure 7

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1991 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. × = station with no *O. bartramii* paralarvae present.

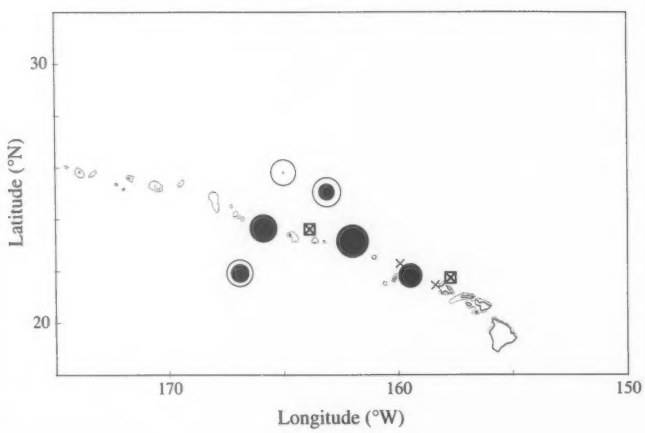

Figure 8

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1991 *Townsend Cromwell* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. ⊠ = station with one *O. bartramii* paralarva present but no mantle length measurement recorded. × = station with no *O. bartramii* paralarvae present.

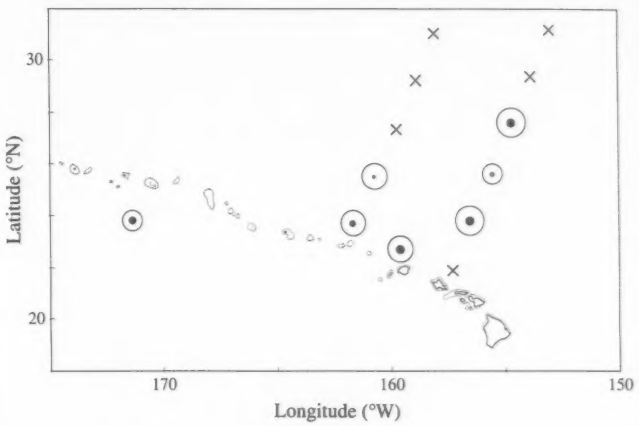

Figure 9

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1992 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. × = station with no *O. bartramii* paralarvae present.

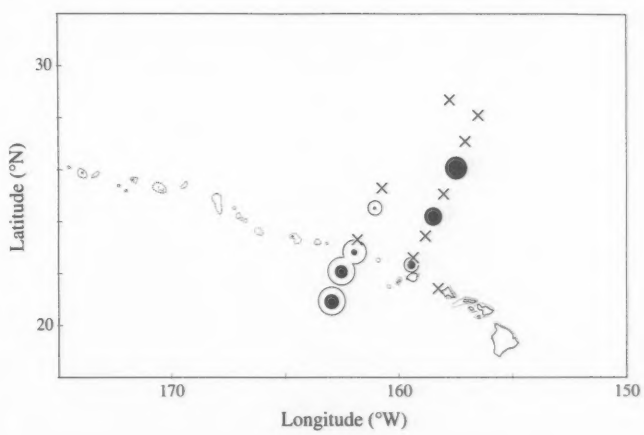

Figure 10

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1992 *Townsend Cromwell* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station. × = station with no *O. bartramii* paralarvae present.

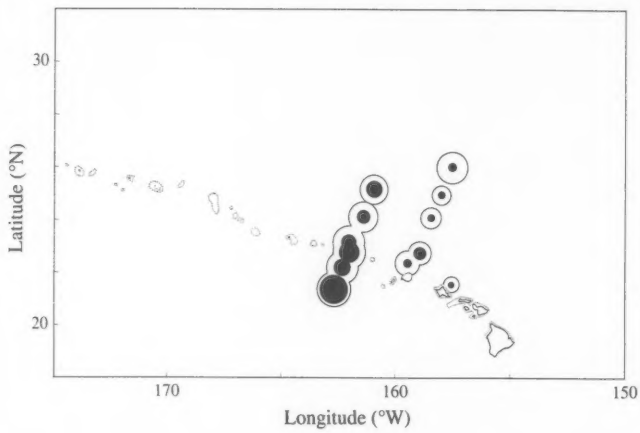

Figure 11

Map of the Hawaiian Archipelago showing the projected spawning grounds of *Ommastrephes bartramii* paralarvae captured during the 1993 *Hokusei Maru* survey. Open circles represent the estimated spawning area for all paralarvae from each station. Closed circles represent the estimated spawning area for the youngest paralarvae from each station.

Table 2

Estimated hatching localities of *O. bartramii* paralarvae relative to the Hawaiian Archipelago (assuming a unidirectional flow away from the archipelago). Stn = station number; DO = station distance from archipelago; Catch = number captured; Min age = age of youngest paralarvae; Max age = age of oldest paralarvae; Max distance traveled = maximum distance the oldest paralarvae could have traveled after hatching; and Minimum distance from land = the closest to the archipelago the largest paralarvae could have hatched. *XX* = indicates spawning of largest animal could have occurred at archipelago. % = percentage of paralarvae of all ages from each station that would have hatched ≥10 km from the archipelago. Cruise total = percentage of paralarvae of all ages from entire survey that must have hatched ≥10 km from the archipelago. Total samples = percentage of paralarvae of all ages from all surveys combined that must have hatched ≥10 km from the archipelago. NC = no increment count.

Stn.	DO (km)	Catch (no.)	Min age (d)	Max age (d)	Max distance traveled (km)	Minimum distance from land (km)	%
***Hokusei Maru* February 1991 survey**							
1	9	2	14.8	14.8	40	*XX*	0
2	16	26	10.7	24.9	62	*XX*	0
3	106	168	4.6	23.7	59	47	100
4	235	56	12.0	21.1	53	182	100
5	349	43	2.2	22.6	56	293	100
6	460	57	8.4	20.5	51	409	100
7	583	16	12.0	24.7	62	521	100
8	33	0	—	—	—	—	—
Cruise total							92
***Townsend Cromwell* February 1991 survey**							
1	228	4	14.8	22.6	56	172	100
2	15	2	22.9	25.6	64	*XX*	0
3	232	59	0.8	21.7	54	178	100
4	207	28	13.2	24.4	61	146	100
5	28	1	NC	NC	—	—	—
6	16	4	26.9	30.1	75	*XX*	0
7	28	0	—	—	—	—	—
8	13	1	19.8	19.8	49	*XX*	0
9	25	1	NC	NC	—	—	—
10	14	0	—	—	—	—	—
Cruise total							93

meters during the day. If spawning was limited to waters near the island chain, a gradient in size with distance from shore would be expected. Presumably smaller animals would be caught nearshore and larger animals farther offshore. No correlation was found between size and distance from shore.

Drifter data confirm the picture of circulation near the Hawaiian Archipelago that flows are complex and highly variable throughout the islands. Although speeds of four drifters were averaged to estimate a general flow speed in the region, determining where particular paralarvae originated could best be deter-

Table 2 (continued)

Stn.	DO (km)	Catch (no.)	Min age (d)	Max age (d)	Max distance traveled (km)	Minimum distance from land (km)	%
***Hokusei Maru* February 1992 survey**							
1	14	0	—	—	—	—	—
2	11	2	6.6	12.6	31	*XX*	0
3	41	0	—	—	—	—	—
4	142	0	—	—	—	—	—
5	235	1	14.8	14.8	37	198	100
6	337	0	—	—	—	—	—
7	471	1	18.7	18.7	47	424	100
8	585	0	—	—	—	—	—
9	713	0	—	—	—	—	—
10	732	0	—	—	—	—	—
11	269	0	—	—	—	—	—
12	181	23	2.2	12.0	30	151	100
13	26	0	—	—	—	—	—
14	25	129	4.6	20.5	51	*XX*	2
15	126	49	10.7	23.7	59	67	100
16	256	37	12.0	23.7	59	197	100
Cruise total							44
***Townsend Cromwell* March–April 1992 survey**							
1	228	65	5.7	17.1	43	185	100
2	52	195	6.6	22.0	55	*XX*	54
3	74	103	4.6	21.1	53	21	100
4	299	38	2.2	22.0	55	244	100
5	526	0	—	—	—	—	—
6	759	0	—	—	—	—	—
7	972	0	—	—	—	—	—
8	1161	0	—	—	—	—	—
9	954	0	—	—	—	—	—
10	709	145	6.6	25.1	63	646	100
11	482	2	3.5	17.1	43	439	100
12	272	8	6.6	24.4	61	211	100
13	61	0	—	—	—	—	—
Cruise total							84
***Hokusei Maru* February 1993 survey**							
1	20	12	4.6	13.2	33	*XX*	0
2	472	6	6.6	26.6	66	406	100
3	341	16	5.7	16.2	40	301	100
4	230	43	5.7	17.5	44	186	100
5	68	20	10.0	19.8	49	19	100
6	15	137	6.6	21.4	53	*XX*	0
7	271	69	13.2	24.4	61	210	100
8	135	18	10.7	25.6	64	71	100
9	15	63	12.0	27.8	69	*XX*	0
10	36	15	16.7	28.6	71	*XX*	0
11	135	53	13.7	27.6	69	66	100
12	207	2	23.7	29.1	73	134	100
Cruise total							51
Total samples							72

mined by sampling near a drifter that had been tracked. Dynamic height variations reveal information about the longitudinal extent of the reversing flows along the Hawaiian Ridge. Measurements from CTD probes support the findings of studies that suggest the existence of bands of fairly strong currents that are immediately adjacent to the windward side of the Hawaiian Ridge and that are flowing in opposite directions (White, 1983; Mysak and Magaard, 1983).

Bower et al.[1] suggested that distribution of *O. bartramii* paralarvae is not related to the position of the Hawaiian Archipelago. The results presented here confirm this and indicate that most paralarvae captured during the five surveys were hatched at least 10 kilometers from shore, so that spawning occurs predominantly in oceanic waters.

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Effects of square-mesh panels in codends and of haulback delay on bycatch reduction in the oceanic prawn-trawl fishery of New South Wales, Australia

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Abstract.—Two experiments were conducted in the New South Wales oceanic prawn-trawl fishery, 1) by comparing catch from a conventional codend with that from two new codend designs with square-mesh panels and 2) by showing the effects on catches of a short delay in haulback of trawls with square-mesh panels. The two new codend designs incorporated panels of netting (85-mm mesh) sewn such that the meshes were square-shaped (measuring 7 × 11 bars) and inserted lengthwise and widthwise into the tops of the anterior sections. Simultaneous comparisons among these designs and a conventional codend showed that both designs performed similarly by significantly reducing the weights of bycatch that would be discarded (by 46% and 38%, respectively) without significantly reducing the catch of the prawn *Penaeus plebejus*. The second experiment showed that juvenile red spot whiting, *Sillago flindersi*, an important commercial finfish, escaped from the square-mesh panels in the trawl during a 10–15 second haulback delay. Trawls without any haulback delay showed no significant reduction in the bycatch of this species. The results are discussed in terms of the probable behavior of fish in the modified trawls and in terms of the implications that factors such as haulback delay may have on the survival of fish escaping through square-mesh panels in codends.

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In many of the world's prawn-trawl fisheries, significant numbers of nontarget organisms (collectively termed "bycatch," sensu Saila, 1983) are caught incidentally with targeted prawns. This bycatch often includes a large and diverse assemblage of small fish, some of which are juveniles of commercially and recreationally important species (for reviews see Saila, 1983; Andrew and Pepperell, 1992; Alverson et al., 1994; Kennelly, 1995). The incidental capture and mortality of large numbers of these juveniles has been of worldwide concern in recent years because it may reduce the potential biomass and yield of stocks that form the basis of other fisheries (Gordon, 1988; Foldren, 1989).

In New South Wales (NSW), Australia, oceanic prawn trawling involves approximately 300 vessels that usually operate during the night from 11 ports. This fishery is valued at approximately A$17 million per annum and primarily targets the eastern king prawn, *Penaeus plebejus*, although a significant proportion of the total income is derived from the sale of legally retained bycatch (termed "byproduct"), which comprises several commercially important species of fish, crustaceans, and cephalopods (see Kennelly et al., 1992). However, a recent survey examining the spatial and temporal distributions and abundances of the catch and bycatch from four ports in this fishery showed that juveniles of commercially important species comprised a significant portion of the bycatch (Kennelly[1]). Athough many of these juveniles showed large temporal and spatial variabilitiy in their occurrence, some (e.g. red spot whiting, *Sillago flindersi*, and eastern blue spot flathead, *Platycephalus caeruleopunctatus*), were consistently caught in large numbers throughout the sampling period. Although there are few data available on the population structure and dynamics of the key bycatch species or on the extent of their post-trawl mortalities, the quantities involved have raised concerns regarding potential detrimental impacts of prawn trawling on future stocks of these species (Kennelly, 1993). We therefore began an investigation that examined various modifications to trawling gear and trawling practices that minimize undesirable bycatch while maintaining catches of prawns and commercial byproduct.

[1] Kennelly, S. J. 1993. Study of the bycatch of the NSW east coast trawl fishery. Final report to the Fisheries Research and Development Corporation, P.O. Box 222, Deakin, ACT, 2600, Australia. Project No. 88/108. ISBN 0 7310 2096 0, 520 p.

One suite of modifications to trawls that has been successful throughout the world in reducing bycatches while retaining the target catch involves the use of square-mesh panels in codends (Robertson and Stewart, 1988; Carr, 1989; Briggs, 1992; Broadhurst and Kennelly, 1994; Robertson[2]; Isaksen and Valdemarsen[3]; Suuronen[4]). Quantifying the effectiveness of square-mesh panels in codends has been approached by a variety of experimental methods. At the simplest level, catches and bycatches from control and modified codends have been compared by using alternate tows (Robertson and Stewart, 1988; Broadhurst and Kennelly, 1994), by towing both codends as twin gear (Briggs, 1992), by using trouser trawls (Walsh et al., 1992; Suuronen[4]), or by towing either gear from two adjacent vessels (Thorsteinsson, 1992). Alternatively, covers of small-mesh netting over modified codends have provided estimates of the quantities of fish escaping (Robertson and Stewart, 1988).

Although these kinds of experiments have determined the effectiveness of square-mesh panels in codends, without direct observations by divers or cameras there is no information available on the patterns of behavior of escaping fish or on the period when escapement occurs during tows. The latter point raises an important issue with respect to the survival rates of escaped catch. Because fish are exhausted to varying degrees owing to the stress associated with capture (see Wardle, 1983; Main and Sangster[5]), the ultimate efficiency of square-mesh panels in reducing bycatch mortality is determined by the rate at which nontarget individuals are excluded. The survival of these individuals is probably inversely proportional to the time spent in the trawl, because studies have shown that fish that remain in the codend are subjected to high levels of stress and fatigue (Main and Sangster[5]; Main and Sangster[6]).

Observations from divers, from video cameras, and from towed submersibles, have provided conflicting information on the behavior of escaping fish (Wardle, 1983, 1989; Watson, 1989; Briggs, 1992; Watson et al., 1993). For example, in the Irish Sea, Briggs (1992) observed that the escape of European whiting, *Merlangius merlangus,* occurred continually throughout the duration of the tow. In contrast, Watson et al's (1993) studies in the Gulf of Mexico showed that red snapper, *Lutjanus campechanus,* maintained their position within the codend throughout the tow and escaped only when haulback was initiated.

In the NSW oceanic prawn-trawl fishery there is commonly a delay of up to 15 seconds (s) between slowing the vessel and engaging the winch to haul in the trawl (termed haulback delay). Because of this delay, possible effects, such as those observed by Watson et al. (1993), need to be investigated prior to interpreting the effectiveness of square-mesh panels in codends. Direct observations of such effects, however, always assume that the divers or cameras have no artificial effects on the behavior of the fish or on the normal commercial operation of the gear. While it may be reasonable to assume minimal effects in conditions with adequate light, Wardle (1989) found that the use of cameras with artificial light at night or in turbid conditions (below 10^{-3} lux) disorientated fish and disturbed their behavior. The possibility of such effects makes this technique unsuitable for assessing the effects of haulback delay on square-mesh panels in the NSW oceanic prawn-trawl fishery which operates at night.

Our specific goals in this experiment were 1) to investigate the effectiveness of square-mesh panels in reducing the bycatch from the NSW oceanic prawn-trawl fishery and 2) via a manipulative experiment, to provide an accurate and inexpensive means to determine the effects of haulback delay on the performance of these designs.

Materials and methods

Two experiments were conducted on commercial prawn-trawl grounds east of Yamba, New South Wales (29°26'S, 153°22'E), between August and October 1994 by using a commercial prawn trawler (13.8 m). Three florida flyers (mesh size 42 mm), each with a headline length of 12.8 m, were rigged in a standard triple gear configuration (see Andrew et al., 1991, for details) and towed at 2.5 knots. Each of the identical outside nets were rigged with zippers (no. 10 nylon open-ended auto lock plastic slides) to facilitate changing of the codends (see Broadhurst et al., in press). Because the middle net was not rigged

[2] Robertson, J. H. B. 1983. Square mesh cod-end selectivity experiments on whiting (*Merlangius merlangus* (L.)) and haddock (*Melanogrammus aeglefinus* (L.)). Int. Counc. Explor. Sea, council meeting 1983/B:25, 13 p. [Mimeo.]

[3] Isaksen, B., and J. W. Valdemarsen. 1986. Selectivity experiments with square mesh codends in bottom trawl. Int. Coun. Explor. Sea, council meeting 1986/B:28, 18 p. [Mimeo.]

[4] Suuronen, P. 1990. Preliminary trials with a square mesh codend in herring trawls. Int. Counc. Explor. Sea, council meeting 1990/B:28, 14 p. [Mimeo.]

[5] Main, J., and G. I. Sangster. 1988. Scale damage and survival of young gadoid fish escaping from the cod-end of a demersal trawl. *In* J. DeAlteris (ed.), Proceedings of selectivity and survivability workshop, p. 17–34. Univ. Rhode Island Sea Grant Advisory Service, Narragansett, RI.

[6] Main, J., and G. I. Sangster. 1991. A study of haddock (*Merlanogrammus aeglefinus* (L.)) behavior in diamond and square-mesh codends. Scot. Fish. Work. Paper 19/91, 25 p.

exactly like the outside nets (see Andrew et al., 1991), it was excluded from our analyses.

The codends used in the experiments measured 75 meshes long (3 m) and were constructed from 40-mm mesh netting (Fig. 1). They comprised two panels. The anterior panel was 100 meshes in circumference and constructed of 25 meshes of 48-ply twine attached to 25 meshes of 35-ply twine. The posterior panel was 200 meshes in circumference and constructed of 3-mm diameter braided twine.

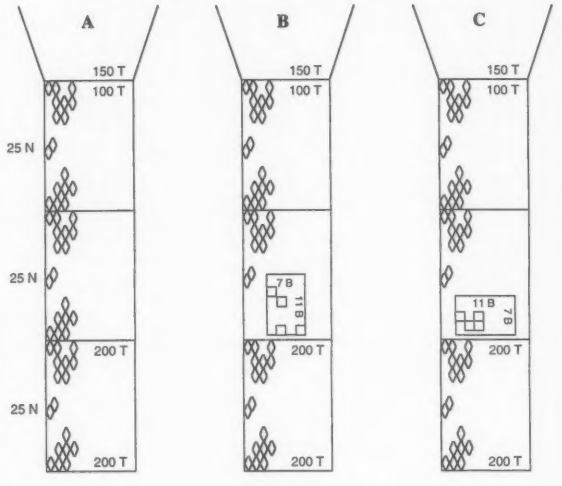

Figure 1

Diagrammatic representation of (**A**) the control codend, (**B**) the 85-mm-long codend and (**C**) the 85-mm-wide codend (T=transversals; B=bars; N=normals).

Experiment 1—evaluation of codends

Three codend designs were compared. The control codend was made entirely of diamond-shaped meshes (Fig. 1A). The second codend (termed the 85-mm-long codend) had a panel of 85-mm netting cut on the bar (7 bars × 11 bars) inserted lengthwise into the top of the anterior section (Fig. 1B). The third codend (termed the 85-mm-wide codend) had the same panel inserted sideways into the top of the anterior section (Fig. 1C).

All three codends were compared against each other in independant, paired trials. That is, in separate tows, the 85-mm-long codend was compared against the control; the 85-mm-wide codend was compared against the control; and the 85-mm-long and 85-mm-wide codends were compared against each other. The particular pair to be compared in a given tow were placed on each outside net of the triple-rigged gear. The position and order of each codend was determined randomly (to eliminate any biases between different nets) and the codends were used in normal commercial tows of 90-min duration (with a haulback delay of 10–15 s) on established prawn-trawl grounds. Over six nights we completed a total of 10 replicate tows of each paired comparison. Prior to the trials and at the end of each night, we rigged the outside nets with normal commercial codends and performed tows to ensure that there were no differences in the fishing characteristics of each net.

Experiment 2—effects of haulback delay

In this experiment the 85-mm-long codend from experiment 1 was tested against the control for possible effects due to haulback delay. The codends were interchanged between tows, and each night we completed two replicate 90-min tows that included 1) a 10–15 s haulback delay (measured as the duration between slowing the vessel and engaging the winch) and 2) no haulback delay. Over 4 nights we completed a total of 8 replicate tows for each type of haulback.

To ensure independence among tows, the location and direction of each tow was randomly selected from the available locations on established grounds northeast of Yamba. The grounds trawled varied in depth and ranged between 20 and 25 fm.

Data collected from the experiments

After each tow in each experiment, the codends were emptied onto a partitioned tray. Prawns and all commercially important species larger than the minimum legal size (retained commercials) were separated from the remaining bycatch. The remaining bycatch (termed discarded bycatch) was then sorted. This included individuals of commercially important species that were smaller than the minimum legal size (discarded commercials). Data collected from each tow were the total weight of prawns and their size (to the nearest 1-mm carapace length); the weight of the discarded bycatch; the weights, numbers, and sizes (to the nearest 0.5 cm) of discarded commercial species and retained commercial species; and the numbers of noncommercial species in the assemblage. All individuals were counted without subsampling. Several commercially important species were caught in sufficient quantities to allow meaningful comparisons. These were eastern king prawn, *Penaeus plebejus*, cuttlefish, *Sepia* sp., Octopus, *Octopus* sp., red spot whiting, *Sillago flindersi*,

eastern blue spot flathead, *Platycephalus caeruleopunctatus*, and smooth bug, *Ibacus* sp.

The paired comparisons done in experiment 1 were analyzed with one-tailed, paired *t*-tests. Data from experiment 2 were analyzed with two-factor analysis of variance (Underwood, 1981) after testing for homogeneity of variances (Cochran's test). Further, treating the data from each haulback-delay period separately, we compared data from the pairing of the 85-mm-long and control codends, using one-tailed, paired *t*-tests. Data from the 85-mm-long codend and its control (which used the haulback delay of 10–15 s in experiment 2) were combined with data from these codends in experiment 1, to provide a larger dataset for analysis of the results for the 85-mm-long codend. Size frequencies of prawns and red spot whiting from both experiments and the combined data were compared by using two-sample Kolmogorov-Smirnov tests (P=0.05).

Results

Experiment 1—evaluation of codends

Both the 85-mm-long and 85-mm-wide codends significantly reduced the weight of discarded bycatch (means reduced by 46% and 38%, respectively) (Fig. 2A; Table 1). The 85-mm-wide codend significantly reduced the number and weight of discarded red spot whiting (by 71% and 75%), and the number of trash species (Fig. 2, D–F; Table 1). There were insufficient data from the 85-mm-long codend to analyze data for red spot whiting (<2 fish per replicate). Neither of the codends with square-mesh panels significantly reduced the catch of prawns (Table 1), although the mean catches were 7.5% lower in the 85 mm long codend and 2.5% lower in the 85-mm-wide codend (Fig. 2G). Apart from a significant reduction in the number of trash species with the use of the 85-mm-long codend (Fig. 2F; Table 1), there were no other detectable differences between the two codends with square-mesh panels. Two-sample Kolmogorov-Smirnov tests comparing the size-frequency distributions for the king prawns and red spot whiting measured from each sample showed no significant differences in the relative size compositions between any of the codends tested.

Experiment 2—effects of haulback delay

There were no significant effects due to haulback delay on the differences in catch between the control and 85-mm-long codends for the weight of bycatch and prawns (Fig. 3, A–B; Table 2). However, haulback delay significantly increased the difference in catch between the control and 85-mm-long codends for the number and weight of red spot whiting and decreased the weight of retained cuttlefish (Fig. 3, C–E; Table 2). There were no significant effects among any of the other variables (i.e. retained octopus, discarded eastern blue-spot flathead, smooth bug, and trash species) due to haulback delay. The number and weight of red spot whiting were significantly differ-

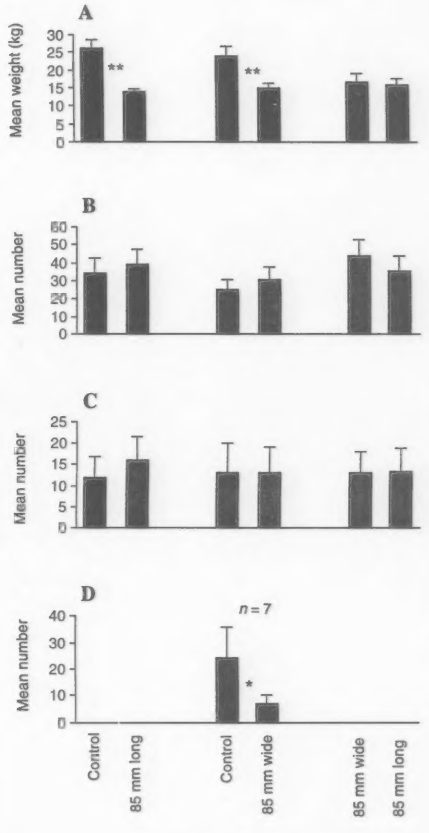

Figure 2

Differences in mean catch (±SE) between each of the codends in experiment 1 (evaluation of codends): (**A**) the weight of discarded bycatch; (**B**) the numbers of retained octopus (*Octopus* sp.); (**C**) the numbers of discarded cuttlefish (*Sepia* sp.); (**D**) the number of discarded red spot whiting (*Sillago flindersi*); (**E**) the weight of discarded red spot whiting (*Sillago flindersi*); (**F**) the number of noncommercial species; and (**G**) the weight of prawns (*Penaeus plebejus*). * = P<0.05; ** = P<0.01; unless stated otherwise, n = 10.

ent among nights in the experiment. No variables displayed significant interactions among haulback delay and nights (Table 2).

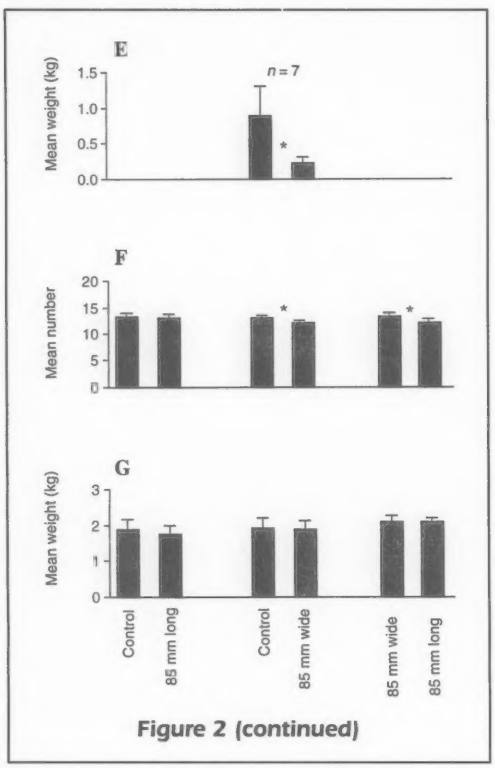

Figure 2 (continued)

One tailed, paired *t*-tests comparing data from the control and 85-mm-long codends showed that the 85-mm-long codend significantly reduced the weight of bycatch and significantly increased the weight of prawns during both a 10–15 s delay and no delay in haulback (Fig. 3, A–B; Table 3). The 85-mm-long codend significantly reduced the number and weight of discarded red spot whiting compared with the control during the 10 to 15 s haulback delay (means reduced by 64% and 56%, respectively) (Fig. 3, D–C; Table 3). There was no significant reduction in these variables for this codend when there was no delay in haulback, although the mean numbers and weights of red spot whiting were reduced by 21% and 25%, respectively (Fig. 3, D–C; Table 3). The weight of retained cuttlefish was significantly decreased in the 85-mm-long codend when there was no delay in haulback (Fig. 3E; Table 3). No other variables showed any differences between the control and 85-mm-long codends either with or without a delay in haulback. Two-sample Kolmogorov-Smirnov tests comparing size-frequency distributions for king prawn and red spot whiting (Fig. 4) measured from each sample showed no significant differences in the relative size compositions between the 85-mm-long and control codends during either a 10–15 s delay or no delay in haulback.

Aggregated data for the 85-mm-long codend

Combining all the data for the 85-mm-long codend, we found that this modification significantly reduced

Table 1

Summary of one-tailed paired *t*-tests comparing number and weight of catch of three different codends. *n* = number of replicates; rsw = red spot whiting.

	Control vs. 85-mm-long			Control vs. 85-mm-wide			85-mm-long vs. 85-mm-wide		
	Paired *t*-value	*P*	*n*	Paired *t*-value	*P*	*n*	Paired *t*-value	*P*	*n*
Weight of prawns	1.458	0.089	10	–0.357	0.635	10	0.000	—	10
Weight of discarded bycatch	6.355	0.0001**	10	5.800	0.0002**	10	0.491	0.317	10
Number of discarded cuttlefish	–2.17	0.971	10	0.638	0.269	9	–0.066	0.526	10
Weight of discarded cuttlefish	–0.656	0.736	10	–0.219	0.584	9	–0.264	0.601	10
Number of retained cuttlefish	0.810	0.219	10	0.819	0.217	10	–1.213	0.871	10
Weight of retained cuttlefish	1.331	0.108	10	–0.599	0.718	10	–0.077	0.530	10
Number of retained octopus	–1.847	0.952	10	–2.202	0.973	10	1.451	0.090	10
Weight of retained octopus	–0.248	0.595	10	–0.972	0.822	10	0.346	0.368	10
Number of discarded rsw	(insufficient data)			2.242	0.033*	7	(insufficient data)		
Weight of discarded rsw	(<2 fish per replicate)			2.223	0.034*	7	(<2 fish per replicate)		
Number of noncommercial sp.	1.246	0.122	10	2.228	0.026*	10	2.283	0.024*	10

*P=<0.05; **P=<0.01.

the weight of bycatch (mean reduction of 37%) and the number and weight of red spot whiting (by 68% and 58%, respectively) (Figs. 5, A–C; Table 4). This codend did not significantly reduce the weight of prawns (although the mean catch was 3% lower) nor any of the other variables (Fig. 5E; Table 4). Two-sample Kolmogorov-Smirnov tests failed to detect any significant difference in the size compositions of prawns between the 85-mm-long and control codends (Fig. 6A). The sizefrequency distributions for red spot whiting, however, were significantly different between these codends (Fig. 6B).

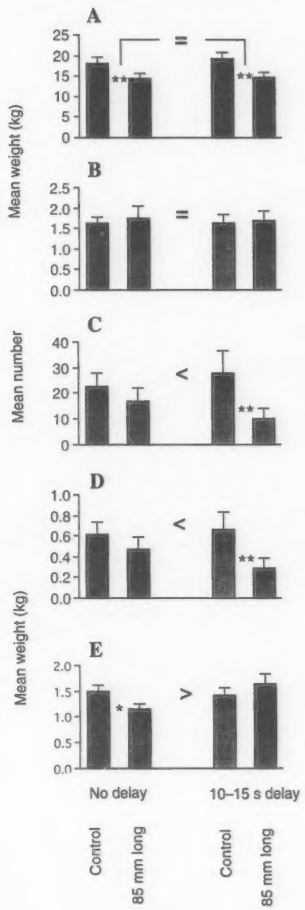

Figure 3

Differences in mean catch (±SE) between the control and 85-mm-long codends in experiment 2 (effects of haulback delay) for no delay and a 10–15 s delay in haulback (<, >, and = indicate direction of differences): (**A**) the weight of discarded bycatch; (**B**) the weight of prawns (*Penaeus plebejus*); (**C**) the number of discarded red spot whiting (*Sillago flindersi);* (**D**) the weight of discarded red spot whiting (*Sillago flindersi*); and (**E**) the weight of retained cuttlefish (*Sepia* sp.). * = $P<0.05$; ** = $P<0.01$.

Discussion

The results of these experiments show that codends with square-mesh panels have the potential to reduce bycatch of nontarget individuals (see also Robertson and Stewart, 1988; Briggs, 1992; Fonteyne and M'Rabet, 1992; Broadhurst and Kennelly, 1994). By experimentally examining the effects of haulback delay, we have also quantified, for the first time, the effects that such operational procedures can have on the escape of some individuals.

In previous experiments, Broadhurst and Kennelly (1994, 1995) showed that square-mesh panels in the anterior sections of codends were effective in releasing small fish (i.e. mulloway, *Argyrosomus hololepidotus*) from prawn trawls in the Hawkesbury River. These results were attributed to the differences in behavior of fish and prawns in their response to

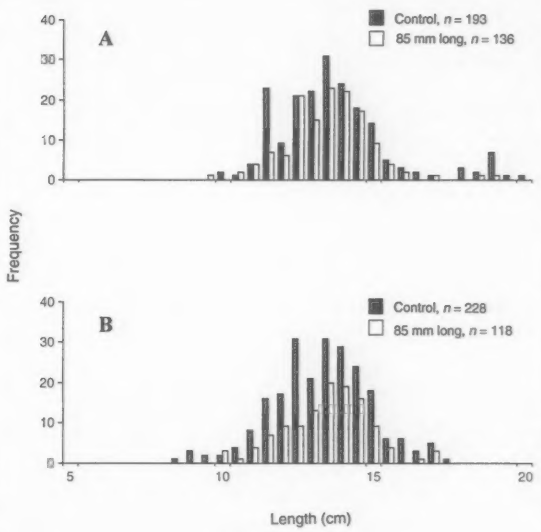

Figure 4

Length-frequency distributions of red spot whiting (*Sillago flindersi*) from the control and 85-mm-long codends for experiment 2: (**A**) during no delay in haulback and (**B**) a 10–15 s delay in haulback.

Table 2

Summary of *F*-ratios from two-way analyses of variance to determine effects on variables (weight and number of catch) due to haulback delay on different nights.

Treatment	df	Prawns (wt.)	Discarded bycatch (wt.)	Retained octopus (no.)	Retained octopus (wt.)	Retained cuttlefish (no.)	Retained cuttlefish (wt.)	Discarded eastern blue spot flathead (no.)	Discarded eastern blue spot flathead (wt.)	Discarded red spot whiting (no.)	Discarded red spot whiting (wt.)	Discarded smooth bugs (no.)	Discarded smooth bugs (wt.)	Trash species (no.)
Haulback delay (HD)	1	0.25	0.93	0.02	0.01	4.86	9.24*	0.13	0.06	8.25*	7.48*	0.26	2.77	0.02
Nights (N)	3	1.83	1.07	0.12	0.03	0.60	0.91	0.28	0.74	6.13*	5.95*	3.74	0.66	0.57
HD × N	3	2.51	2.26	0.21	1.13	1.78	0.60	0.44	0.96	0.156	0.58	1.07	0.48	1.30
Residual	8													

*$P<0.05$.

Table 3

Summary of one-tailed paired *t*-tests for the effect of haulback delay on weight and number of catch for control and 85-mm-long codends. $n = 8$ for all comparisons; rsw = red spot whiting; ebs = eastern blue spot flathead.

	No haulback delay		10–15 second haulback delay	
	Paired *t*-value	*P*	Paired *t*-value	*P*
Weight of prawns	0.903	0.198	–0.595	0.715
Weight of discarded bycatch	7.976	0.0001**	4.610	0.001**
Number of retained octopus	–0.242	0.592	–0.043	0.516
Weight of retained octopus	1.560	0.081	0.979	0.180
Number of retained cuttlefish	1.964	0.045*	–1.085	0.844
Weight of retained cuttlefish	2.694	0.015*	–1.843	0.946
Number of discarded ebs	–0.403	0.951	–0.989	0.823
Weight of discarded ebs	–0.956	0.815	–0.712	0.751
Number of discarded rsw	1.072	0.159	3.464	0.0005**
Weight of discarded rsw	0.778	0.231	3.984	0.002**
Number of discarded smooth bugs	–0.037	0.639	–0.716	0.752
Weight of discarded smooth bugs	–0.333	0.626	–0.477	0.676
Number of noncommercial sp.	0.477	0.334	0.174	0.433

*$P<0.05$; **$P<0.01$.

stimuli from the trawl and to the hanging configurations of the codends. Fish were apparently herded together at the taper of the codend, invoking an escape response to the sides and top of the net. The attachment of an anterior panel of 100-mesh circumference to a posterior panel constructed of heavy twine and 200-mesh circumference, presumably created a back pressure of water that was directed out through the open anterior square meshes, facilitating the escape of fish. This sequence of events was assumed to occur continually throughout the duration of the trawl. The response of prawns to this stimuli appeared fairly limited; other studies have shown that prawns are not capable of maintaining active escape responses to the trawl and are quickly forced against the meshes and towards the back of the codend (Lochhead, 1961; Main and Sangster, 1985; Newland and Chapman, 1989).

The two square-mesh codends used in experiment 1 were designed to take advantage of the theory discussed above by incorporating a panel of square mesh on top of the anterior section only, so that small fish might escape without a reduction in the catch of prawns or of larger commercially important bycatch

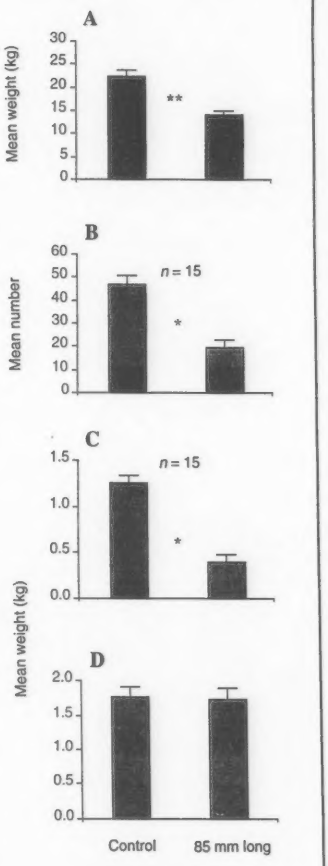

Figure 5

Differences in mean catch (± SE) between the control and 85-mm-long codend, combined across both experiments: (**A**) the weight of discarded bycatch; (**B**) the number of discarded red spot whiting, *Sillago flindersi;* (**C**) the weight of discarded red spot whiting, *Sillago flindersi;* and (**D**) the weight of prawns *Penaeus plebejus*. * = $P<0.05$; ** = $P<0.01$; unless stated otherwise $n = 18$.

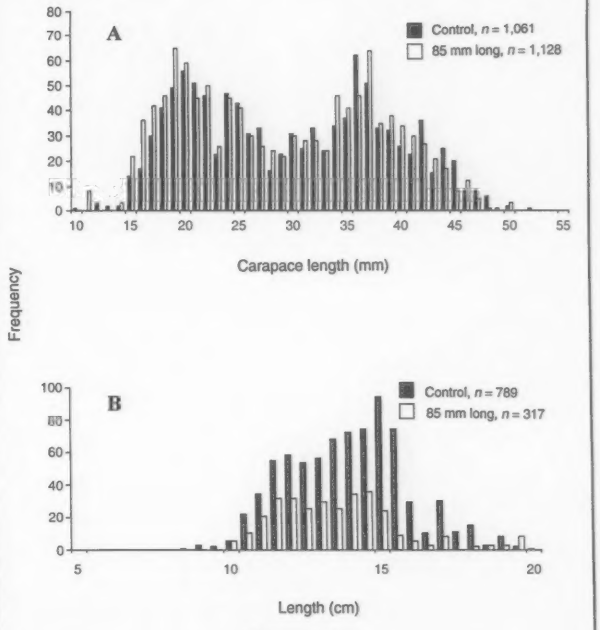

Figure 6

Length-frequency distributions of (**A**) king prawn, *Penaeus plebejus,* and (**B**) red spot whiting, *Sillago flindersi,* from the control and 85-mm-long codends combined across experiments.

species. Both the 85-mm-wide and 85-mm-long codends performed similarly, significantly reducing the weight of discarded bycatch (by 48% and 38% respectively) with no significant reduction in the weight of prawns or retained species (Fig. 2; Table 1). The 85-mm-wide codend also significantly reduced the number and weight of red spot whiting by 71% and 75%, respectively (Fig. 2; Table 1), whereas, based on the aggregated data, the 85-mm-long codend reduced these by 68% and 58%, respectively (Fig. 5; Table 4).

Experiment 2 compared the differences between the control and 85-mm-long codends with and without a short (10–15 s) delay during haulback. The results suggest that the individuals comprising discarded bycatch escaped continually throughout the duration of the tow (Fig. 3A; Table 2). Their behavior and escape from the square-mesh panel may be explained, therefore, according to the theory discussed above. For red spot whiting, however, there was no significant reduction in number or weight when there was no delay in haulback (although the means were reduced by 21% and 28%, respectively), but there was a significant reduction of 64% and 56.6%, respectively, for the tows that included a 10–15 s delay (see Figs. 3 and 6; Table 3). Red spot whiting, therefore, did not appear to exhibit the same behavior as the other species because the majority of these fish appeared to escape during the 10–15 s delay in haulback.

Table 4

Summary of one-tailed, paired *t*-tests comparing control and 85-mm-long codends trialed with a 10–15 s haulback delay, combined over both experiments. *n* = number of replicates; rsw = red spot whiting.

	Control vs. 85-mm-long		
	Paired *t*-value	*P*	*n*
Weight of prawns	1.000	0.165	18
Weight of discarded bycatch	5.720	0.0001**	18
Number of retained cuttlefish	0.355	0.363	18
Weight of retained cuttlefish	0.566	0.289	18
Number of retained octopus	–0.948	0.822	18
Weight of retained octopus	–0.169	0.566	18
Number of discarded rsw	1.935	0.036*	15
Weight of discarded rsw	2.185	0.023*	15
Number of noncommercial sp.	1.587	0.065	18

*$P<0.05$; **$P<0.01$.

A possible reason why few red spot whiting escaped continuously during trawling is that there were insufficient stimuli generated in the codend to invoke an escape response. This hypothesis is supported by previous studies that have shown that physiological and behavioral differences between species are major factors in the effectiveness of escape panels (Robertson and Stewart, 1988; Briggs, 1992; Fonteyne and M'Rabet, 1992). The subsequent escape of red spot whiting from the 85-mm-long codend during the 10–15 s haulback delay may have been a result of additional stimuli generated by changes in the geometry of the codend. For example, Watson (1989) observed that during haulback, differences in the contours of the codend and associated water flow caused fish to aggregate and become disorientated. The fish then increased their swimming speeds and randomly charged the meshes around the codend. By opening the meshes in this area (i.e. by our inclusion of the 85-mm-long square-mesh panel), we may have stimulated some fish to escape the trawl.

The delayed escape of red spot whiting from the 85-mm-long codend raises important questions concerning the extent of their mortality during trawling and after escape. Because previous studies have shown that fish that remain in the codend experience greater stress and fatigue than those that escape continuously, those individuals escaping at the end of the tow may suffer greater mortality. Further, such post-trawl mortality, particularly among smaller fish, may increase in proportion to tow duration. Obviously such effects on red spot whiting should be investigated prior to commercial use of the 85-mm-long codend per se, because, unless most of the escaping fish survive, such designs are of little value.

It may be possible to reduce the problems of trawl mortality for red spot whiting by altering the design of the 85-mm-long codend so that more fish escape continuously during trawling. One possible modification to the design would be to make the square-mesh panel longer (see Briggs, 1992), allowing more red spot whiting to escape at random along the codend. This may also provide juveniles of other commercially important species (i.e. cuttlefish, octopus, and eastern blue spot flathead) the opportunity to escape, although there was little evidence in our experiments to suggest that these species displayed active escape response toward the square-mesh panel (see Figs. 2 and 3; Tables 1–3). Their lack of exclusion is more likely attributable to intraspecific variability in behavioral responses rather than to the design of the square-mesh panel (see also Robertson and Stewart, 1988; Briggs, 1992).

Another modification to allow more red spot whiting to escape the trawl continuously may be to increase the size of mesh used in the panels. However, the size-frequency composition of red spot whiting captured in the 85-mm-long codend and control showed that the size of mesh used in the panel allowed fish within the range of sizes sampled to escape, including some individuals of commercial size (>16 cm) (Fig. 4). Further, this size of mesh resulted in no significant reduction in the weight of prawns, nor were there any significant differences detected in the size composition of prawns between the control and the 85-mm-long or 85-mm-wide codends. Subsequent increases in the size of mesh may, there-

fore, result in further loss of commercial red spot whiting and possibly some reduction in the catch of prawns.

The square-mesh codends tested in these experiments provide further evidence of the effectiveness of this type of exclusion device in reducing the bycatch of unwanted species, while maintaining the catch of prawns and other species of commercial size. Further, for a fishery that retains a range of species, these designs offer a relatively simple and inexpensive method for eliminating a large part of the incidental catch. It is evident from the results, however, that not all species to be excluded behave in a similar manner and that the effects of operational procedures such as haulback delay can significantly influence the rate of exclusion of some species. Therefore, it is imperative that future research into exclusion designs, such as square-mesh panels, include an assessment of such operational factors so that the full impact of bycatch excluders on reducing the mortality of incidentally caught juveniles can be assessed.

Acknowledgments

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Revision of the frigate tunas (Scombridae, *Auxis*), with descriptions of two new subspecies from the eastern Pacific

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Abstract.—Two cosmopolitan species of frigate tunas, *Auxis thazard* (Lacepède) and *A. rochei* (Risso), are differentiated primarily by the width of the corselet under the origin of the second dorsal fin and by the anterior extent of the dorsal scaleless area above the pectoral fin. *Auxis thazard* has five or fewer scales in the corselet under the second dorsal fin, and the dorsal scaleless area extends anterior to the tip of the pectoral fin; *A. rochei* has six or more scales and the dorsal scaleless area does not reach the tip of the pectoral fin. Of nine morphometric characters examined with ANCOVA, four body depth measurements were significantly different between the species. *Auxis rochei* is a slender species with each of the four body depth measurements approximately equal, whereas *A. thazard* is more tuna-shaped, with a deeper, more robust body and with more unequal body depth measurements. For both species, eastern Pacific populations differ from Atlantic and Indo-West Pacific populations at what we consider the subspecific level. The eastern Pacific *A. thazard brachydorax* new subspecies has more gill rakers, usually 43–48 vs. usually 38–42 in *A. t. thazard*. Body depth at anal-fin origin, pectoral-fin length, and corselet width were also significantly different between *A. thazard brachydorax* and *A. t. thazard*. The eastern Pacific *A. rochei eudorax* new subspecies has an even wider corselet than that of *A. rochei rochei*, usually more than 20 scales wide compared with 6–19 scales.

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It is not clear whether there are one or two species of frigate tunas of the genus *Auxis*. In the Indo-West Pacific region, several investigators have distinguished a narrow-corseleted species (N) from a wide-corseleted species (W): Bleeker (1854, 1855) from the East Indies as *A. tapeinosoma* (N) and *A. thynnoides* (W); Kishinouye (1915, 1923) from Japan as *A. hira* (N) and *A. maru* (W); Wade (1949) from the Philippines and Jones (1958) from India as *A. thazard* (N) and *A. tapeinosoma* (W); and Matsumoto (1960a) from Hawaii as *A. thazard* (N) and *A. thynnoides* (W). However, most Atlantic-based workers have considered the frigate tunas to be a single worldwide species which they have identified as *Auxis thazard* (Dresslar and Fesler, 1889; Jordan and Evermann, 1896; Fraser-Brunner, 1950; Rivas, 1951; Zavala-Camin, 1983). Fitch and Roedel (1963) have shown that there are two sympatric species of frigate tunas in the Indo-West Pacific: the narrow-corseleted *A. thazard* (Lacepède) and the wide-corseleted *A. rochei* (Risso) (Fig. 1). They used the name *A. rochei* for the wide-corseleted species on the supposition that only one species occurred in the Mediterranean Sea and Atlantic Ocean and that *rochei* was the earliest name for it. Richards and Randall (1967) have shown that both species occur in the Atlantic, reopening the question of the proper name for Atlantic *Auxis*.

Frigate tunas (*Auxis*) are the smallest members of the tribe Thunnini, the true tunas. *Auxis rochei* reaches a fork length (FL) of 600 mm and *Auxis thazard*, at least 420 mm. To date, frigate tunas have not been greatly exploited, partly because of their small size. Of the total world catch of tunas, bonitos, and billfishes in 1993 (4,654,750 metric tons (t), FAO, 1995), only 4.5% (208,305 t) was *Auxis*. The largest landings are by Asian countries (Philippines 110,357 t; Thailand 36,300 t; Japan 27,896 t; and India 15,684 t). *Auxis* has soft meat and is not suitable for sashimi (slices of raw fish) because of its strong astringent taste, probably due to the high level of free amino acids in the meat (Murata et al., 1994). At least as larvae, *Auxis* are widespread and very abundant (Yabe et al., 1963, fig. 15; Ahlstrom, 1971; Ramíriz-Estévez and Ornelas-

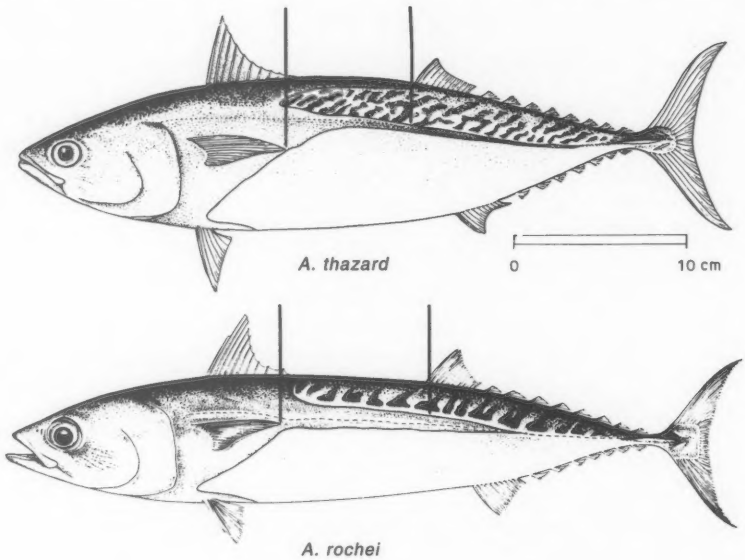

Figure 1

Auxis thazard (top) and *A. rochei* (bottom) showing anterior extent of dorsal scaleless area in relation to distal end of pectoral fin (left line) and width of corselet under origin of second dorsal fin (right line).

Roa, 1991). Richards (1984:28) concluded that *Auxis* "... is the most widely distributed and abundant scombrid in tropical seas." With stocks of other tuna species continually diminishing, there is increased potential for greater exploitation of *Auxis*. Before exploitation increases, it is necessary to establish how many species exist and what their correct names are, to determine how to identify them, and to obtain some idea of the major worldwide populations.

Fitch and Roedel (1963) also showed that the eastern Pacific populations of both species differed significantly from the Indo-West Pacific populations but did not name them pending further work. We confirm Fitch and Roedel's findings that the eastern Pacific population of *A. thazard* has more gill rakers (usually 43–48) than other populations (usually 38–42 in Atlantic and Indo-West Pacific populations), similar to the counts for *A. rochei*. The eastern Pacific population of *A. rochei* has an even wider corselet (usually more than 20 scales wide under the second dorsal fin) than other populations (8–19 scales in populations from the Indo-West Pacific).

This paper distinguishes the two species. We have located the type specimen of *rochei* and designate a neotype for *thazard* to stabilize current use of these names for these species. We evaluate the systematic status of eastern Pacific populations of the two species and describe them as new subspecies, *Auxis thazard* ***brachydorax*** and *Auxis rochei* ***eudorax***.

Materials and methods

Methods follow those used by Collette and Gillis (1992), in a revision of the double-lined mackerels *Grammatorcynus*, and by Collette and Russo (1985) in a revision of the Spanish mackerels *Scomberomorus*. Morphometric characters used in this study are as follows: FL (fork length); HdL (head length); P1L (pectoral-fin length); P1T (distance from pectoral-fin tip to anterior edge of dorsal scaleless area above lateral line); and CW (corselet width under second dorsal-fin origin). Owing to the different shapes of *A. rochei* and *A. thazard*, we postulated that four body depth measurements would illustrate these differences: 1Dor (body depth at origin of first dorsal); 1Dend (body depth at posterior end of first dorsal); 2Dor (body depth at origin of second dorsal); and Aor (body depth at anal-fin origin). *Auxis rochei* is a more slender species and the four body depth

measurements are approximately equal, whereas *A. thazard* is more tuna-shaped, having narrow entering and departing wedges and more unequal body depths.

Morphometric data were analyzed with regression analysis, analysis of covariance (ANCOVA), and principal component analysis (PCA). Regression analysis was run on the combined morphometric data for all populations of *A. rochei* vs. the combined populations of *A. thazard* to determine whether morphometric differences exist between species. Regression analyses were also run on morphometric data for major populations of each species to look for intraspecific differences. The following combinations of geographic populations were tested: for *A. rochei*—western Atlantic (n=36) vs. Mediterranean (n=34) plus eastern Atlantic (n=64), western Pacific (n=82) vs. eastern Pacific (n=37); for *A. thazard*—Gulf of Guinea (n=20) vs. Indian Ocean (n=38), western Pacific (n=75) vs. central Pacific (n=17), and westcentral Pacific (n=92) vs. eastern Pacific (n=69).

PCA was performed with the character variables FL, 1Dor, 1Dend, 2Dor, and Aor to determine whether these characters supported species level separation of *A. rochei* from *A. thazard* and separation between the eastern Pacific population and the other populations for both species. Very little separation was observed with PCA because 97.9% of the variation is explained by principal component 1. This means that almost 98% of the variation can be explained by differences in size, whereas only a little more than 2% of the variation can be explained by character differences among the different populations.

ANCOVA was performed on the variables 1Dor, 1Dend, 2Dor, Aor, P1L, and CW with size (FL) as the covariate to determine whether these characters differentiated *A. rochei* from *A. thazard* and to see whether eastern Pacific populations of each species were different from other populations. ANCOVA showed that morphometric data for each species were the same for all populations, except for the eastern Pacific, and could be combined. For each species, the combined populations were run against the eastern Pacific population to test the level of differentiation of the eastern Pacific population. For *A. rochei,* the combined populations we tested against the eastern Pacific (n=30) were western Atlantic (n=36), Gulf of Guinea (n=64), Mediterranean (n=34), Indian Ocean (n=9), and western Pacific (n=82). For *A. thazard,* the combined populations we tested against the eastern Pacific (n=63) were Indian Ocean (n=38), western Pacific (n=71), central Pacific (n=17), and Australia (n=4).

Material examined is listed at the end of each subspecies account and includes 267 specimens of *A. thazard* and 291 specimens of *A. rochei*. Abbreviations of institutions housing the material examined follow Leviton et al. (1985). CMFRI is the Central Marine Fisheries Research Institute, Cochin, India. ZRC is the current institutional code for the Zoological Reference Collection at the National University of Singapore.

Systematics

Auxis Cuvier, 1829

Auxis Cuvier, 1829:199. Type-species: *Scomber rochei* Risso, 1810, by subsequent designation of Gill, 1862

Diagnosis (Modified from Collette, 1979.) *Auxis* lacks the prominent paired fronto-parietal fenestra in the top of the skull found in all the other tunas, tribe Thunnini (except *Allothunnus*). The dorsal and ventral branches of the cutaneous artery originate separately from the dorsal aorta in *Auxis* (Godsil, 1954); a common cutaneous artery divides into dorsal and ventral branches laterally from the dorsal aorta in the other Thunnini. The ventral branch is very poorly developed, less so than in other Thunnini. The dorsal cutaneous artery lies ventral to the corresponding vein in *Auxis;* it lies dorsal in *Euthynnus* (Godsil, 1954). The vertebral column differs from all other scombrids in having a long pedicel or epihaemal process (1.5–2 times the centrum depth) that forces the dorsal aorta to run much further ventrally from the vertebral column than in other tunas. The interpelvic process is single and very long, equal to or longer than the pelvic fins themselves; it is shorter than the pelvic fins in all other Scombridae.

Description Body robust, elongate, and rounded. Teeth small and conical, in a single series. Two dorsal fins, the first with 10–12 spines, separated from the second by a long interspace (at least equal to length of first dorsal-fin base), the second fin followed by 8 finlets; pectoral fins short; anal fin followed by 7 finlets. Gill rakers 36–49. Body naked except for the corselet, which extends posteriorly along the lateral line past the origin of the second dorsal fin. In *A. thazard*, the extension is only 1–5 scales wide beneath the second dorsal fin, in *A. rochei* it is six scales or more. A strong central keel is present on each side of the caudal-fin base between two smaller keels. Vertebrae: 20 precaudal plus 19 caudal, total 39. Color: dorsum bluish, turning to deep purple or almost black on the head; belly white, usually without stripes or spots, occasionally black spots present on

belly between pectoral and pelvic fins as in *Euthynnus*; pectoral and pelvic fins purple, their inner sides black.

Relationships *Auxis* is related most closely to *Euthynnus* (Kishinouye, 1923; Collette, 1979, 1984; Finnerty and Block, 1995). It has been considered (Collette, 1979) to be the most primitive member (except for *Allothunnus*) of the Thunnini, the true tunas, because it lacks the frontoparietal fenestra present in *Euthynnus, Katsuwonus*, and *Thunnus,* because its subcutaneous circulatory system is more poorly developed than that of the more advanced tunas, and because *Auxis* shows no suturing of the first vertebra to the skull as is present in higher Thunnini. Tunas have a pair of lateral retia which serve the red muscle and act as heat exchangers enabling them to maintain body temperatures several degrees warmer than ambient water (3.5–9.5°C, mean 5.9°C, in the case of *Auxis,* Schaefer, 1985). In addition, *Auxis* and *Euthynnus* share a large central heat exchanger below the vertebral column in a series of enlarged haemal arches. *Auxis* is endothermic at sizes of 200 mm FL and larger (Dickson, 1994). The liver is similar to that in *Euthynnus* in having a very long right lobe running the length of the body cavity (Fig. 2). Prominent branches of the hepatic vein are present on the ventral surface of the liver lobes in both genera. *Auxis* differs from *Euthynnus* in having a greatly reduced left liver lobe; the left and middle lobes are of about equal length in *Euthynnus.* A swimbladder is present in larvae but degenerates by 20 mm as in *Euthynnus* and *Katsuwonus* (Richards and Dove, 1971).

Osteological comparisons Several authors (Kishinouye, 1923; Watanabe, 1962, 1964; Yoshida and Nakamura, 1965; Chi and Yang, 1972; Uchida, 1981; Zavala-Camin, 1983) have reported osteological differences between the species. Watanabe (1962, 1964) found that there were two types of *Auxis* based on long and short parapophyses. The differences were more prominent in specimens larger than 111 mm, especially on the 25th and 27th vertebrae. *Auxis thazard* had long free parapophyses, whereas *A. rochei* (as *A. tapeinosoma*) had short free parapophyses. In addition, in young *A. thazard* the first free parapophysis is developed mostly on the 23rd vertebra, and the first inferior foramen occurs on the 27th or 28th vertebra. In young *A. rochei,* however, the first free parapophysis is usually produced on the 21st or 22nd vertebra, and the first foramen occurs on the 29th or 30th vertebra. Other differences between the two species were the ratio of the caudal vertebral length to precaudal vertebral length and the ratio of body height at anal-fin origin to length from first dorsal to second dorsal origin. Yoshida and Nakamura (1965) found that in *A. thazard* the length of the anterior branch of the haemal process of the 24th to the 28th vertebra was longer and contacted the preceding arch. In *A. rochei* the anterior branches of the haemal processes were short, more fragile, and were never in contact with the preceding haemal arches. The angle between the temporal crests and a line parallel to the supraoccipital crest ranged from 0 to 2 degrees in *A. rochei* and from 3 to 7 degrees in *A. thazard.* In skulls of the same length, skulls of *A. thazard* were wider than those of *A. rochei.*

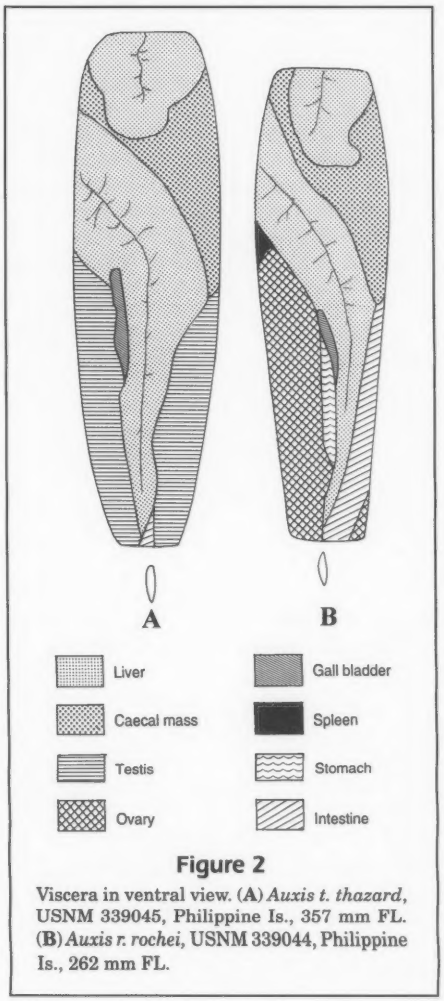

Figure 2

Viscera in ventral view. (**A**) *Auxis t. thazard*, USNM 339045, Philippine Is., 357 mm FL. (**B**) *Auxis r. rochei*, USNM 339044, Philippine Is., 262 mm FL.

Larval differences In several geographic regions, workers have been able to divide their material of larval and juvenile *Auxis* into what appear to be two

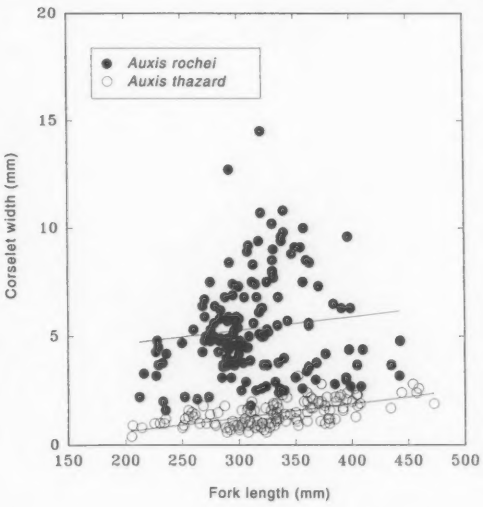

Figure 3

Corselet width under second dorsal-fin origin vs. fork length in *Auxis rochei* (closed circles, $y = 0.005x + 3.933$, r=0.09) and *A. thazard* (open circles, $y = 0.006 - 0.673$, r=0.62).

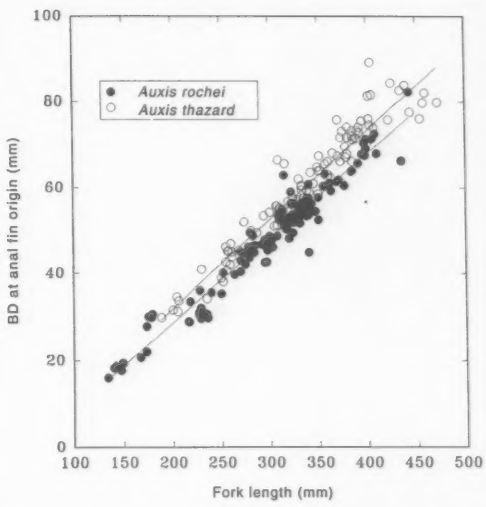

Figure 4

Body depth (BD) at anal-fin origin in *Auxis rochei* (closed circles, $y = 0.17x - 3.06$, r=0.92) and *A. thazard* (open circles, $y = 0.207x - 9.58$, r=0.96).

species (Wade, 1949, Philippines; Matsumoto, 1959; Gorbunova, 1969, 1974, Indian and Pacific oceans; Zhao et al., 1982, and Sun et al., 1986, China; Richards, 1989, western central Atlantic). Juveniles have been successfully identified (e.g. Wade, 1949), but larvae are more difficult to identify to species because the corselet scales and gill rakers that distinguish the adults are not fully developed in the larvae. For brief length intervals, pigment characters are useful in distinguishing two types of larvae.

Gorbunova (1974) distinguished between larvae of the two species. *Auxis rochei* is characterized by a seemingly slower rate of development and a shallower body depth. The relative size of the eye is smaller and the pigmentation on the caudal peduncle is less intense. *Auxis thazard* is distinguished by a more rapid rate of development, a greater body depth, a shorter caudal portion of the body, and more intense body pigmentation. Richards (1989) emphasized the presence of pigment along the lateral line in the posterior part of the body in *A. rochei* and its absence in *A. thazard*.

Biochemical differences The first attempts to separate the two species of *Auxis* biochemically were by Matsumoto (1960b) who found that Hawaiian specimens could be distinguished in a one-dimensional chromatogram. Taniguchi and Nakamura (1970) examined muscle protein of *A. thazard* and *A. rochei* by the cellulose acetate electrophoretic method. They found five components in the electropherograms of both species, but some components were not common to both. Electrophoretic patterns of the two species were clearly distinguishable from each other by the mobility and percentage of each component. Taniguchi and Konishi (1971) used starch gel electrophoresis to detect protein specificity between *A. thazard* and *A. rochei*. No individual variation occurred in the electropherograms of 11 specimens of *A. thazard*, whereas all 170 specimens of *A. rochei* fit into 1 of 3 phenotypic patterns. They hypothesized that these three phenotypes are controlled by two codominant alleles. Distribution of the three phenotypes was independent of age and sex.

Auxis thazard (Lacepède, 1800)

Frigate tuna

Diagnosis *Auxis thazard* has a narrow corselet that is 0.5–3.5 mm, usually 0.5–1.0 mm wide (Fig. 3) but no more than five scales wide under the second dorsal-fin origin (Table 1), a greater body depth at the anal-fin origin (Fig. 4), and the anterior margin of the scaleless area above the corselet extends anteriorly beyond the tip of the pectoral fins (Figs. 1 and 5) unlike that in *A. rochei*. Color pattern: 15 or more

Table 1

Number of corselet scales under second dorsal-fin origin in populations of *Auxis*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	*n*	$\bar{x}$
A. t. thazard																																
W. Atlantic	—	—	4	1	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	7	4.0
E. Atlantic	1	2	10	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	2.9
Indian O.	1	3	23	7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	34	3.1
W. Pacific	14	7	25	5	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	53	2.5
C. Pacific	—	—	11	3	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	16	3.4
																															124	2.7
A. t. brachydorax																																
E. Pacific	13	8	42	2	3	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	68	2.6
Galapagos	—	—	1	1	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	5	5.6
																															73	2.8
A. r. rochei																																
W. Atlantic	—	—	—	—	2	8	4	7	4	1	—	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	30	7.9
Mediterranean	—	—	—	—	—	—	3	2	1	5	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	13	9.2
E. Atlantic	—	—	—	—	—	—	—	4	3	2	2	9	6	6	3	4	4	3	3	2	1	2	—	1	—	—	—	—	—	—	55	14.3
Indian O.	—	—	—	—	—	—	1	—	—	3	2	3	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	10	11.5
W. Pacific	—	—	—	—	—	—	—	1	—	10	1	7	3	6	6	1	1	—	1	—	—	—	—	—	—	—	—	—	—	—	37	12.6
																															148	11.7
A. r. eudorax																																
E. Pacific	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1	1	1	—	2	8	3	2	2	3	—	—	1	1	1	29	21.6

narrow, oblique to nearly horizontal, dark wavy lines in the scaleless area above the lateral line (Figs. 1 and 6). Spots sometimes occur between the pectoral and pelvic fins (see Robins and Ray, 1986: pl. 48), as they usually do in *Euthynnus*.

Geographical distribution Probably cosmopolitan in warm waters (Fig. 7) but there have been relatively few documented occurrences in the Atlantic Ocean. Although we did not examine specimens of either species from the southeastern Atlantic and although Zavalla-Camin (1983) concluded that there was only a single variable species, both species do occur there as can be seen from the anterior extent of the dorsal scaleless area (Fig. 8, 20 specimens of *A. thazard* and 33 specimens of *A. rochei*). On the basis of two specimens of *A. thazard* from Haifa, Israel (HUJ 17480, HUJ 17826) provided by Dani Golani, we believe both species occur in the Mediterranean Sea.

Habitat and biology (From literature summarized in Uchida, 1981, and Collette and Nauen, 1983:29.) An epipelagic, neritic, and oceanic species. In the eastern Pacific, mature fish occur throughout the

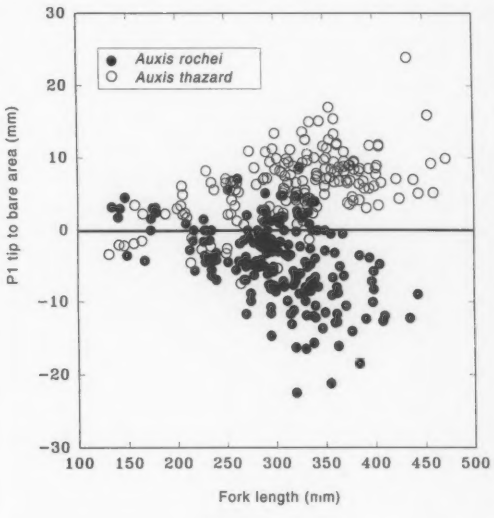

Figure 5

Distance from the tip of the pectoral fin (P1) to the bare area above the lateral line in *Auxis rochei* (closed circles) and *A. thazard* (open circles).

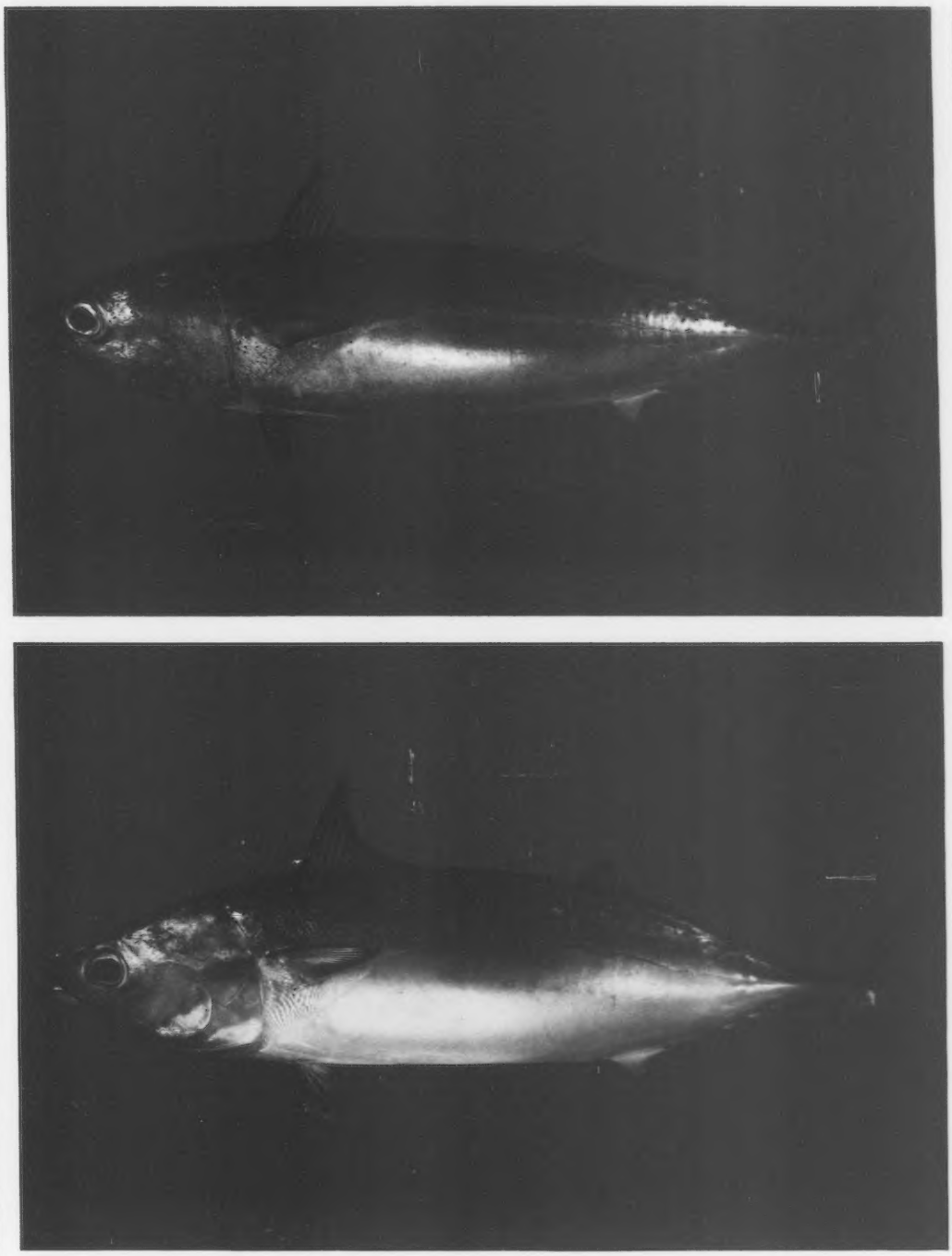

Figure 6

(**Upper photograph**) *Auxis rochei rochei*, 283 mm FL, Indonesia, Bali, Padang Bai; 28 Feb 1984; John E. Randall. (**Lower photograph**) *Auxis thazard thazard*, 267 mm FL, Hawaii, Oahu; 11 Nov 1994; John E. Randall.

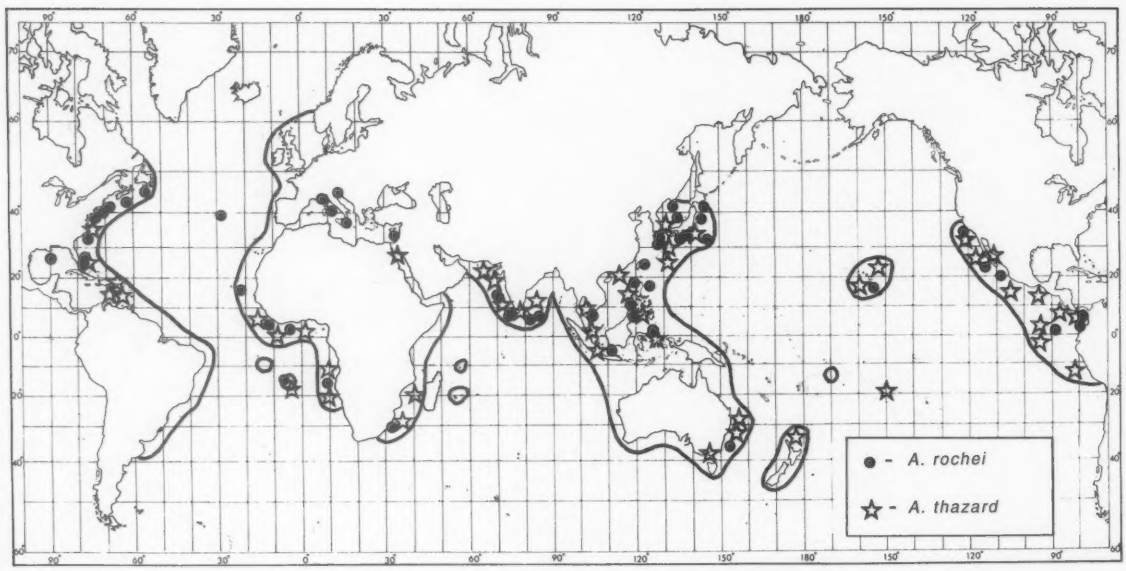

Figure 7

Distribution of *Auxis rochei* and *A. thazard*. Solid lines show approximate limits of distribution; symbols indicate localities of specimens examined.

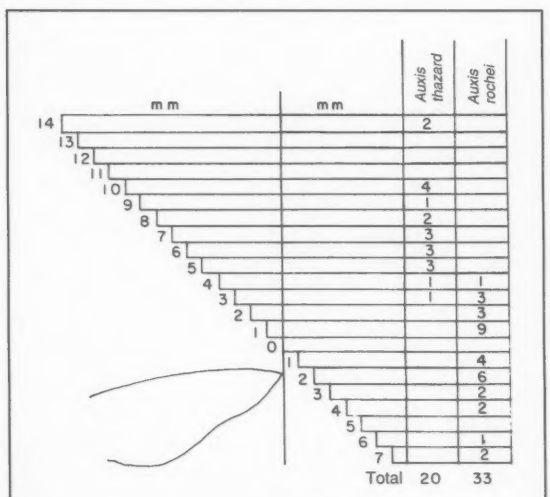

Figure 8

Distance from the tip of the pectoral fin to the anterior extent of the dorsal scaleless area above the lateral line in *Auxis* from southeastern Brazil (from Zavala-Camin, 1983: fig. 4). The scaleless area extends 3–14 mm anterior to the tip of the pectoral fin in 20 specimens of *A. thazard* but falls short of the pectoral-fin tip or extends slightly anterior to it in 33 specimens of *A. rochei*.

year; although off Costa Rica spawning is heaviest from December through April, whereas in Japanese waters it peaks in July as expressed by the index of sexual maturity. In the southern Indian Ocean, the spawning season extends from August to April; north of the equator it is reported from January to April. Fecundity was estimated at about 1.37 million eggs per year in a 44.2-cm-long female. Fecundity of fish in Indian waters ranged between approximately 200,000 to 1.06 million eggs per spawning in correlation with size of females.

Size Maximum fork length from drift net records in the Indian Ocean is 510 mm, but off Sri Lanka it is 580 mm; common lengths range between 250 and 400 mm FL depending on gear type and may also vary seasonally and by region. Size at first maturity is reported at about 290 mm FL in Japanese waters but at about 350 mm around Hawaii. *Auxis thazard* grows to be larger than *A. rochei*.

Subspecies The eastern Pacific population of *A. thazard* has more gill rakers, leading us to describe it as a separate subspecies. Linear regression analyses of morphometric characters for *A. thazard* showed significant differences between the eastern Pacific and the remaining combined populations in four char-

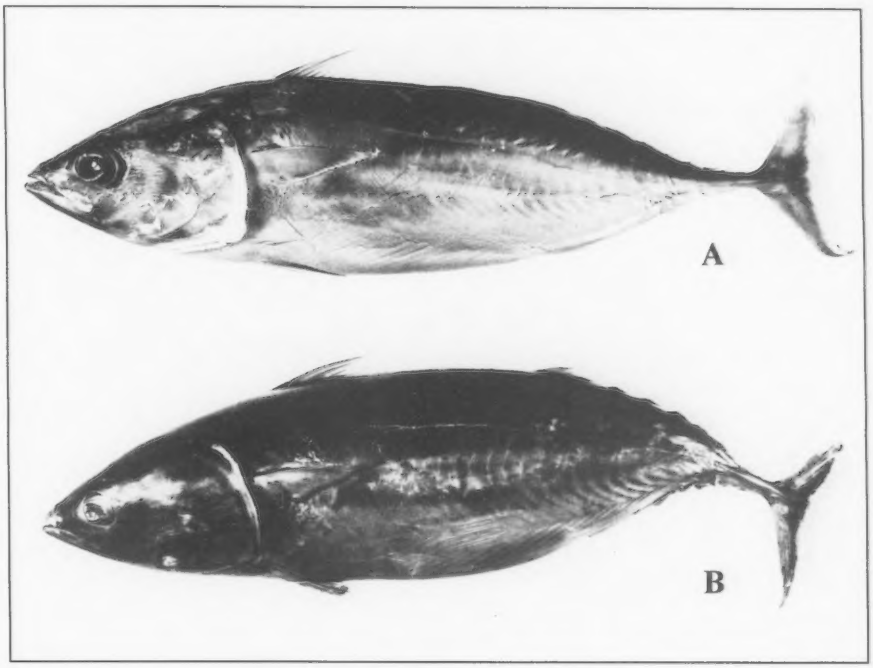

Figure 9

Type specimens of *Auxis thazard*. (**A**) Neotype of *Scomber thazard* Lacepède, 1800; USNM 265418; 274 mm FL; Indonesia, Moluccas, Halmahera I. (**B**) Holotype of *Auxis thazard brachydorax* n. ssp.; USNM 320406; 352 mm FL; 7°51'N, 99°51'W.

acters: CW, P1L, 2Dor, and Aor. ANCOVA showed differences that were significant at the 0.01 level of significance for three morphometric characters: AOR, P1L, and CW, further supporting recognition of an eastern Pacific subspecies of *A. thazard*.

Auxis thazard thazard (Lacepède, 1800)

Fig. 9A

Scomber thazard Lacepède, 1800:599 (original description) Lacepède, 1801:9–13 (description, off New Guinea); no type-specimens extant.

Auxis taso Commerson, 1831 *in* Cuvier and Valenciennes, 1831:146–148 (original description based on *Scomber taso* Commerson, New Guinea).

Auxis tapeinosoma Bleeker, 1854:408–409 (original description, Nagasaki, Japan); holotype: RMNH 6050 (see Boeseman, 1964:465, pl. 3, fig. 10).

Auxis thazard: Dresslar and Fesler, 1889:434 (synonymy, in part). Jordan and Evermann, 1896:867–868 (synonymy, in part). Wade, 1949:230–231, fig. 1 (comparison of both species, Philippines), figs. 3–6 (juveniles, 23.1–57.2 mm FL). Fraser-Brunner, 1950, synonymy, in part:152. Jones, 1958:190–192 (India). Matsumoto, 1960a:174–175, fig. 2 (comparison of both species, Hawaii). Jones and Silas, 1961:377–378, fig. 3. Fitch and Roedel, 1963:1329–1342, fig. 1 (generic review). Jones and Silas, 1963:1781–1786; 1964:20–22 (India). Tortonese, 1963 (Mediterranean population differs from Indo-Pacific populations of wide-corseleted *Auxis*). Richards and Randall, 1967:245–247, fig. 1 (first western Atlantic records). Chi and Yang, 1972 (osteology, morphology, Taiwan). Richards and Klawe, 1972:68–69 (references to eggs and young). Uchida, 1981 (species synopsis). Gorbunova, 1974:48–50 (description of larvae, Pacific and Indian oceans, fig. 12). Collette and Nauen, 1983:30–31 (synonymy, description, distribution, fig.). Robins and Ray, 1986:261 (W. Atlantic), pl. 48 (color fig.). Richards, 1989:32–33 (description of larvae, western central Atlantic; figs. of 7 larvae 4.5 mm NL to 25.0 mm SL).

Table 2

Number of gill rakers in populations of *Auxis*.

	36	37	38	39	40	41	42	43	44	45	46	47	48	49	*n*	$\bar{x}$
A. t. thazard																
Western Atlantic	—	—	1	1	2	2	1	—	—	—	—	—	—	—	7	40.1
Eastern Atlantic	—	—	1	4	6	5	5	—	1	—	—	—	—	—	22	40.6
Indian Ocean	1	2	6	8	7	7	3	1	—	—	—	—	—	—	35	39.6
Western Pacific	—	1	18	18	28	20	9	—	1	—	—	—	—	—	95	39.8
Central Pacific	—	—	—	3	9	7	9	—	—	—	—	—	—	—	28	39.3
Total															187	39.8
A. t. brachydorax																
Eastern Pacific	—	—	—	—	1	1	7	14	19	13	13	6	2	—	76	43.3
Galapagos	—	—	—	—	—	—	—	2	1	1	—	—	2	—	6	45.2
Total															82	43.4
A. r. rochei																
Western Atlantic	—	—	—	1	3	7	11	8	2	2	1	—	—	—	34	43.4
Eastern Atlantic	—	—	—	—	1	8	12	16	26	10	6	2	—	—	81	43.5
Mediterranean	—	—	—	—	1	10	8	8	6	3	—	1	—	—	37	42.6
Indian Ocean	—	—	—	—	—	—	—	1	3	—	1	3	2	—	10	45.8
Western Pacific	—	—	—	—	—	—	1	7	12	29	21	6	3	1	80	45.2
Central Pacific	—	—	—	—	—	—	—	3	3	5	1	1	—	—	13	44.5
Total															255	44.0
A. r. eudorax																
Eastern Pacific	—	—	—	—	—	—	—	1	5	11	5	5	3	—	30	45.6
Total																

Auxis hira Kishinouye, 1915:23–24, fig. 16 (original description, Japan); no type-specimens known. Kishinouye, 1923:462–463, pl. 31, fig. 55 (anatomy).

Diagnosis *Auxis thazard thazard* has fewer gill rakers, 36–44, usually 38–42 (Table 2); a greater body depth at the anal-fin origin (Fig. 10); a longer pectoral fin (Fig. 11); and a wider corselet (Fig. 12) than has *A. thazard brachydorax*.

Description Corselet narrow under second dorsal-fin origin (1–6 scales, usually 3, Table 1). Dorsal scaleless area extends anteriorly beyond P1 tip (1–16 mm, usually 3–12 mm, Fig. 5). Width of corselet under second dorsal-fin origin 0.5–3.5 mm, usually 0.5–1.0 mm (Fig. 3).

Types

Scomber thazard Lacepède, 1800. Neotype USNM 265418 (274 mm FL), Indonesia, Moluccas, Halmahera I., 0°58'N, 127°56'E; 12 Mar 1979; herein designated. Pectoral fin 41.2 mm, anterior extent of dorsal scaleless area 10.9 mm anterior to tip of pectoral fin, width of corselet under second dorsal-fin origin 1.4 mm, 3 scales in corselet under second dorsal-fin origin, gill rakers 10 + 31 = 41. Fig. 9A.

Auxis tapeinosoma Bleeker, 1854. Holotype RMNH 6050 (200 mm FL), Japan, Nagasaki; S.N. Wolff. Pectoral fin 20.5 mm; 2 scales in corselet under second dorsal fin origin; gill rakers 10 + 30 = 40. Photograph of type presented by Boeseman (1964, pl. 3, fig. 10).

Material examined 194 specimens (44.8–472 mm FL) from 94 collections.

Western Atlantic 10 specimens (240–471 mm FL) from 10 collections.

CAS SU 10874 (1, 305); Massachusetts; D.S. Jordan. USNM 23347 (1, 343); MA, Provincetown; Aug 1879; S.F. Baird. USNM 325226 (1, 449); NC, Oregon Inlet. UF 42693 (1, 344); NC, off Morehead City; 3 Jun 1973; G.F. Burgess. UF 38841 (1, 402); FL, Government Cut off Miami; 31 Jul 1971; T. Iwamoto. UF 98890 (1, 240); FL, Marquesas Keys, 24°29'N, 83°00'W; 23 Sep 1992; G.F. Burgess 92-5. UF 46979 (1, 253); Puerto Rico. USNM 325457 (1, 471); Caribbean, west of St. Vincent, 13°16'N, 62°32'W; 27 Mar 1966; RV *Undaunted*, cr. 2, sta. 114 (skeleton). USNM 325238 (1, 426); 10°47'N, 67°03'W; 24 Mar 1966; RV *Geronimo*, cr. 7, sta. 116. MNHN A.5792 (1, 248); Martinique; Plee; paralectotype of *Auxis vulgaris* Valenciennes.

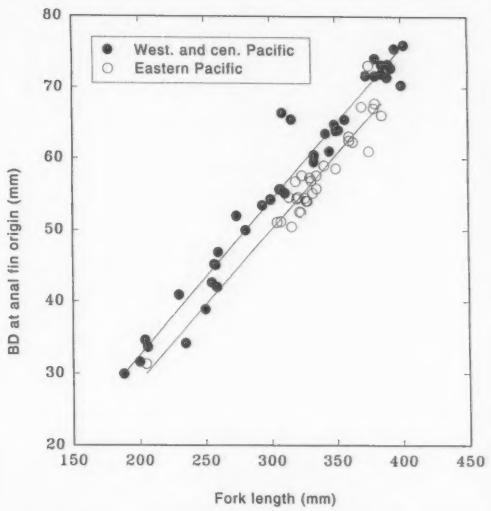

Figure 10

Body depth (BD) at anal-fin origin. Western and central Pacific *Auxis thazard thazard* (closed circles, $y = 0.216x - 10.683$, r=0.98) differ significantly (F=52.06, P<0.00) from eastern Pacific *A. t. brachydorax* (open circles, $y = 0.210x - 13.147$, r=0.96).

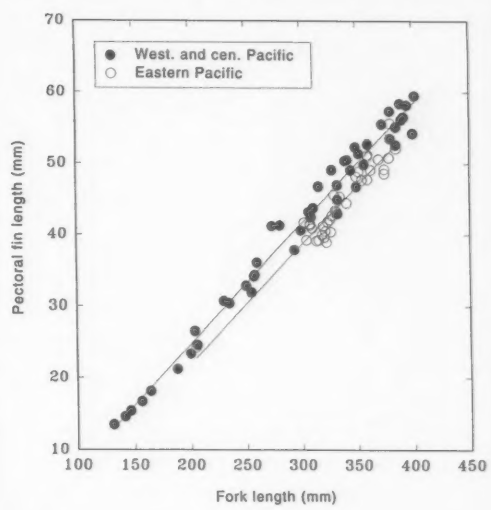

Figure 11

Pectoral-fin length. Western and central Pacific *Auxis thazard thazard* (closed circles, $y = 0.169x - 9.045$, r=0.991) differ significantly (F=24.06, P<0.00) from eastern Pacific *A. t. brachydorax* (open circles, $y = 0.165x - 11.11$, r=0.95).

Eastern Atlantic 24 specimens (261–472 mm FL) from 7 collections.

BMNH 1946.5.23.13–14 (2, 340–383); St. Helena; Colman. HUJ 17480 (1, 323); Mediterranean Sea, purchased in the market at Haifa, Israel; 8 Jun 1993; D. Golani. HUJ 17826 (1, 335); Haifa Bay; 2 Feb 1995; D. Golani. USNM 325237 (1, 442); 5°44'N, 14°28'W; 23 Feb 1965; RV *Geronimo*, cr. 5, sta. 124. USNM 325216 (10, 386–472); Gulf of Guinea; 15 Oct 1967; MV *Caribbean*, set 1. USNM 325956 (1, 261); Ghana; 5 Oct 1967. USNM 325224 (8, 370–439); off Lobito, Angola; fall 1968; MV *Bold Venture*.

Indian Ocean 38 specimens (216–416 mm FL) from 18 collections.

USNM 266918 (1, 310); Israel, Eilat; 21 May 1962. USNM 266919 (1, 330); Israel, Eilat; 1949. USNM 166908 (3, 310–338); Egypt, Ghardaqa; E. Clark. USNM 307773-5 (5, 351–373); north of Tulear, Madagascar, 22°10'S, 43°10'E; 4 Dec 1988; RV *Vityaz* 2657; B.B. Collette 1889. ANSP 93093 (1, 330); Natal coast; 1927; H.W. Bell Marley. CMFRI uncat (1, 415); India, Bombay, Sasson dock; 26 Oct 1979. CMFRI uncat (4, 325–387); India, Mangalore, Kaup; 15 Sep 1979. CMFRI uncat (2, 318–338); India, Vizhinjam; 17 Dec 1979. CMFRI uncat (2, 313–315); India, Veraval. CMFRI uncat (1, 368); India, Veerapandyan patnam, Tuticorin; 23 Oct 1979. CMFRI uncat (1, 416); India, Cochin fishing harbor; 1 Sep 1979. CMFRI uncat (5, 325–360); India, Calicut, off Vellayil; 25 Nov 1979; RSLM Haridas sta. 98. CMFRI uncat (1, 216); India, Cochin fish-

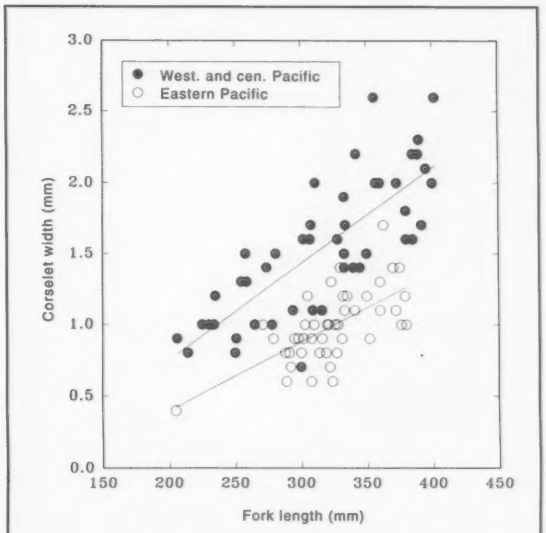

Figure 12

Corselet width under second dorsal-fin origin. Western and central Pacific *Auxis thazard thazard* (closed circles, $y = 0.007x - 0.606$, r=0.79) differ significantly (F=65.94, P<0.00) from eastern Pacific *A. t. brachydorax* (open circles, $y = 0.005x - 0.561$, r=0.65).

ing harbor; 22 Sep 1979. CMFRI uncat (1, 340); India. CMFRI uncat (1, 340); India, northwest Indian Ocean; 25 Mar 1977; MURAENA sta. 78. CMFRI uncat (1, 235); India, Cochin fishing harbor; 22 Sep 1979. USNM 218963 (1, 378); Ceylon, Trincomalee, St. John's market; 13 Sep 1969; P.C. Heemstra. USNM 215024 (6, 252–287); Ceylon; P.C. Heemstra.

Dissections 4 specimens (312–401 mm FL) from 4 collections.

USNM 307773-5 (3, 365–373); Madagascar, north of Tulear; 4 Dec 1988; RV *Vityaz* 2657; B.B. Collette 1889. CMFRI uncat (1, 401); India, Cochin fishing harbor.

Western Pacific 94 specimens (44.8–415 mm FL) from 50 collections.

RMNH 6050 (1, 200), Japan, Nagasaki; holotype of *Auxis tapeinosoma* Bleeker. ZUMT 2475 (1, 234); Japan, Nagasaki Pref.; Aug 1909. ZUMT 23751 (1, 251); Japan, Kagoshima Pref., Taniyama, Kagoshima City; 3 Jul–15 Aug 1930. ZUMT 31281 (1, 334); Japan, Shimane Pref., Matsue; 19 Oct 1935. ZUMT 31286 (1, 302); Japan, Shimane Pref.; 19 Oct 1935. ZUMT 50160 (1, 278); Japan, Nagasaki Pref., Nakadori I., Goto I., Arikawa; 17 Oct 1953. ZUMT 54923-4 (2, 225–250); Japan, Shizuoka Pref., Izu Peninsula; 12 Sep 1981; M. Aizawa. ZUMT 23979 (1, 214); Japan, Kagoshima Pref., Shibushi. CAS SU 24006 (1, 208); Japan, Wakanoura; 1900; Jordan and Snyder. USNM 325231 (1, 308); Japan, south of Tokyo (purchased in Tokyo market); 20 Sep 1966; R.H. Gibbs. USNM 44894 (1, 333); Japan. FMNH 57450 (1, 294); Japan, Sendai; D.S. Jordan. FMNH 57353 (2, 235–250); Japan, Osaka; D.S. Jordan. NMW 14528 (1, 300); Japan; 1900; D.S. Jordan. NMW 14530 (1, 309); Japan, Nagasaki; 1895. ZUMT 16740 (1, 265); Japan, Okinawa Island, Onnason. FMNH 55727 (1, 395); Korea, Fusan; 1911; D. S. Jordan. USNM 325230 (5, 349–402); Hong Kong; Nov 1967; CSM, cr. 10/67. ZRC 3736 (1, 370), South China Sea, 2°15'N, 104°45'E; 26 Mar 1973; RV *Changi*, SEAFDEC. CAS SU 13685 (2, 343–353); Philippine Is., Jolo; 1931; Herre. CAS SU 26430 (1, 238); Philippine Is., Culion; 1931. CAS SU 14524 (1, 263); Philippine Is., Luzon; 1934; Herre. CAS SU 28284 (1, 250); Philippine Is., Culion; Apr 1931; Herre. USNM 218964 (3, 307–342); Philippine Is.; 17 Sep 1963. USNM 150084 (3, 255–258); Philippine Is., Cebu; F. Baker. USM 325232 (1, 260); Philippine Is., Palawan; 25 May 1962; I. Ronquillo. USNM 325235 (3, 200–206); Philippine Is., Manila Bay; 27 May 1962. USNM 339045 (3, 265–357); Phillipine Is., Manila markets; 1–10 Oct 1995; B.B. Collette. CAS 53833 (3, 131–146); Philippine Is., Luzon, Batangas Prov., Batangas market; 24 Apr 1948; Herre. CAS 49634 (2, 156–164); Philippine Is., Batangas Prov., Batangas; 30 Jun 1948. LACM 45781-2 (14, 44.8–75.0); Philippine Is., Luzon, Batangas Bay, Bauan; 27 Mar 1949; M.A. Sabado and D. Leonicio. LACM 45782-2 (3, 62.7–69.2); Philippine Is., Luzon, Batangas Bay, Bauan; 12 Mar 1949; M.A. Sabado and D. Leonicio. LACM 45780-1 (3, 55.8–114); Philippine Is., Luzon, Batangas Bay, Bauan; 27 Sep 1949; M.A. Sabado and D. Leonicio. ZRC 3288 (1, 390); Singapore; Jun 1964; A.K. Tham. ROM 22971 (1, 188); Singapore; 1962–1963; C.C. Linsey. USNM 72629 (1, 230); Java, Batavia; 2 Apr 1909; Bryant and Palmer. SIO 61-735 (3, 206–215); Java Sea, Sunda Straits, 5°37'S, 106°02'E; 22 Mar 1961; Naga Expedition; T. Matsui. BMNH 1892.4.6.74 (1, 257); N. Celebes; Meyer. BMNH 1858.4.21.512 (1, 223); Amboina; Franks. USNM 265418 (1, 274); Moluccas, Kampung Loleba, Wasile district, Halmahera I., 0°58'N, 127°56'E; 12 Mar 1979; neotype of *Scomber thazard* Lacepède and USNM 330940 (1, 281), same data. USNM 215015 (1, 273); Australia, New South Wales, Sydney fish market; 17 Apr 1970; B.B. Collette 1469B. USNM 176970 (1, 300); Australia, New South Wales; Col. Howard. AMS IB 6430 (1, 403); Australia, Botany Bay, New South Wales; Mar 1963; D. Cleaver. AMS IB 845-6 (2, 282–290); Australia, Port Jackson; 3 Feb 1963; Stead. AMS I.21568-001 (1, 355); Australia, New South Wales, Sydney Harbour. AMS I.28544-001 (1, 415); Australia, New South Wales, Long Reef, 33°45'S, 151°19'E; D. Mercer. BMNH 1896.6.17.43 (1, 365); Melbourne market; Degen. NMNZ 9905 (2, 340–357), New Zealand, off Cape Brett, 35°10'S, 174°20'E. NMNZ 6939-42 (4, 290–350); New Zealand area; 16 Apr 1975. NMNZ 7326 (2, 370–372); New Zealand area.

Dissections 2 specimens (312–376) from 2 collections.

USNM 269056 (1, 312); Australia, Port Marquarie, New South Wales; 3 May 1970; B.B. Collette 1474E. USNM 269055 (1, 376); Australia, New South Wales; 17 Apr 1970; B.B. Collette 1469A.

Central Pacific 29 specimens (50.0–400 mm FL) from 10 collections.

LACM 6706-1 (4, 340–400), 6706-2 (4, 333–390), and 6706-3 (4, 345–385); Hawaiian Is. LACM 45778-1 (1, 93.0); Hawaii off Kona; 4 Oct 1962; RV *Charles M. Gilbert* 60-24. LACM 45779-2 (11, 50.0–60.3); Hawaiian Is.; 17 May 1969; RV *Townsend Cromwell* 43-30. CAS SU 12759 (1, 342); Hawaiian Is.; 1901; U.S. Fish Commission. USNM 52748 (1, 259); Hawaii; Bur. Fish. NMW 14529 (1, 316); Hawaii, Honolulu fish market; 1928; Pietschmann. BPBM 35799 (1, 267); Hawaii, Lanai, Cape Kaea; 30 Nov 1957; RV *John R. Manning*, cr. 38. MCZ 26298 (1, 392); Society Is.

Auxis thazard brachydorax Collette and Aadland, new subspecies

Fig. 9B

Diagnosis *Auxis thazard brachydorax* has more gill rakers, 40–48, usually 43–48 (Table 2), a shallower body depth at the anal-fin origin (Fig. 10), a shorter pectoral fin (Fig. 11), and a narrower corselet (Fig. 12) than *A. thazard thazard*.

Description Corselet narrow under second dorsal-fin origin (1–8 scales rows wide, usually 1–3, Table 1). Dorsal bare area extends anteriorly beyond tip of pectoral fins. Width of corselet under second dorsal 0.5–3.5 mm, usually 0.5–1.0 mm (Fig. 3).

Etymology We use the name that Fitch and Roedel used in their manuscript, *brachydorax* from the Greek *brachys* (short) and *dora* (hide) in reference to the narrow corselet. Carl L. Hubbs suggested this

name in a memo dated 1 Feb 1951 to W.I. Follett, concerning an edition of their California fish list, with copies to Fitch and Roedel.

Material examined 73 specimens (205–400 mm FL) from 29 collections.

Holotype USNM 320406 (352 mm FL); 7°51'N, 99°51'W; Olympia; 16 Aug 1991. Pectoral fin 48.9 mm, anterior extent of dorsal scaleless area 10.0 mm anterior to tip of pectoral fin, width of corselet under second dorsal-fin origin 0.9 mm, 3 scales in corselet under second dorsal-fin origin, gill rakers 10 + 35 = 45. See Fig. 9B.

Paratypes from the eastern Pacific 48 specimens (205–400 mm FL) from 21 collections.

LACM 6711-2 (1, 335); CA, Orange Co., 1–2 mi off Huntington Beach; 19 Sep 1960. LACM 34069-1 (1, 330); CA, between Oceanside and San Clemente; 30 Sep 1972. LACM 34254-1 (1, 379); CA, off San Onofre; 20 Jul 1974; MV *Bonanza*. SIO 73-60 (1, 321); CA, La Jolla. SIO 60343 (1, 321); CA, San Diego, off Coronado Hotel. CAS 56979 (2, 355); Baja California, below Holcombe Point; 25 Jul 1958; IATTC. SIO 91-138 (10, 327–350); Baja California, 26°05'N, 113°22'W; 12 Sep 1991; W. Mesa. LACM 34022-1 (1, 205); Baja California, Morgan Bank; Apr 1969; MV *Beverly Lynn;* R. Chikami. LACM 6714-1 (10, 271–302); Baja California, Morgan Bank. SIO 61-257 (2, 312–328); Gulf of California, Ceralbo I., 24°08'N, 104°51.5'W; 22 Jun 1961; W. Baldwin. LACM 6708-1 (1, 335); Gulf of California, 450 Fathom Bank; 24 Mar 1950; MV *Nancy Rose*. CAS 56981 (3, 350–370); Mexico, Sinaloa, 30 mi off Mazatlan; Apr 1951; MV *Gaston Explorer;* field number W 51-151. ANSP 89064 (1, 363); Mexico, Tres Marias, Cleofa I.; 4 Jul 1941; Fifth Vanderbilt Expedition. LACM 6709-5 (2, 360–372); 20°16'N, 105°59'W; 24 Nov 1951; R.C. Wilson 51-S-87. ANSP 89066 (1, 350); Mexico, Colima, 18°00'N, 105°47'W; 29 Jun 1941; Fifth Vanderbilt Expedition. SIO 79-256 (2, 322–328); 15°30'N, 93°30'W; 10 Apr 1974. LACM 6709-2 (1, 376); Gulf of Panama, 9°48'N, 86°00'W; 13 Nov 1951; field number 51-S-82. SIO 80-172 (1, 342); 9°20'N, 94°27'W. LACM 6709-4 (1, 333); Gulf of Panama; field number 51-S-85. USNM 334062 (3, 303–310); 7°51'N, 99°51'W; Olympia; 16 Aug 1991. SIO 58-83-43A (2, 374–395); Peru; 1958; Tomlinson.

Other material examined 26 specimens (305–385 mm FL) from 4 collections.

LACM 6711-8 (4, 360–380); "California"; Jun–Jul 1951; MV *Courageous*. LACM 6711–9 (4, 355–385); "California." UMMZ 160954 (1, 375); "from Mexico"; 16 Sep 1927; L.E. Herr and L.A. Walford. USNM 325223 (17, 305–341); eastern Pacific, exchange from LACM, no other data.

Galapagos Islands 6 specimens (315–400 mm FL) from 4 collections.

LACM 6713-1 (3, 358–375); Isabella I., 5 mi south of Point Cristobal; 8 Mar 1954; MV *Mayflower;* H. Clemens. LACM 39622-1 (1, 385); Skipjack Bank, 01°11'N, 91°03'W; 7 Dec 1952; H. Clemens. ANSP 71417 (1, 315); Charles I.; Feb 1957; South Pacific Expedition; G. Vanderbilt. CAS 56980 (1, 400); Galapagos; Dec 1951; MV *Golden West*; Field Number W51-276.

Auxis rochei (Risso, 1810)

Bullet tuna

Diagnosis *Auxis rochei* has a wider corselet under the second dorsal-fin origin, 5 or more scales wide, usually 7–15 (Table 1), and the anterior margin of the scaleless area above the corselet does not reach the tip of the pectoral fin (Fig. 1). Color pattern: 15 or more fairly broad, nearly vertical dark bars in the scaleless area above the lateral line (Figs. 1 and 6).

Geographical distribution Cosmopolitan in warm waters (Fig. 7). Both species occur off southeastern Brazil (see distribution of *A. thazard*). Most confirmed records of *Auxis* from the Mediterranean Sea are *A. rochei*, with the exception of two specimens of *A. thazard* from Haifa, Israel.

Habitat and biology (From literature summarized in Uchida, 1981, and Collette and Nauen 1983:30.) An epipelagic, neritic, and oceanic species. The spawning season may vary regionally depending on the hydrographical regime. In many parts of the Mediterranean and in the Straits of Gibraltar, maturing fish are common from May onwards, and more than 30% are spent by September. In large areas of the Gulf of Mexico, peaks of batch spawning are reported from March to April and from June to August, whereas in coastal waters from Cape Hatteras to Cuba and in the Straits of Florida, the spawning season begins in February. Indirect evidence suggests that the season extends at least from June through July off Taiwan and from May through August off southern Japan, as indicated by gonad indices and larval counts, respectively. Fecundity ranges between 31,000 and 103,000 eggs per spawning according to size of the fish. Food consists largely of small fishes, particularly anchovies and other clupeids (Etchevers, 1976).

Size Maximum fork length is 500 mm in Japanese catches, commonly to 350 mm. Common fork lengths in the Indian Ocean range between 150 and 250 mm. Fork length at first maturity off Gibraltar is 350 mm for females and 365 mm for males (Rodríguez-Roda, 1966).

Subspecies The eastern Pacific population of *A. rochei* has more scales in the corselet under the second dorsal fin: therefore we describe it as a separate subspecies. ANCOVA on morphometric characters for populations of *A. rochei* were not significant, possibly because of the small size range (300–365 mm) for the eastern Pacific sample, but no significant differences

were found between morphometric features for the eastern Pacific population and other populations.

Auxis rochei rochei (Risso, 1810)

Fig. 13, A and B

Scomber Rochei Risso, 1810:165–167 (original description, Nice); holotype MNHN A. 5808, Nice).

Scomber Bisus Rafinesque, 1810a:45, pl. II (upper fig.) (original description, Sicily); no type material. Rafinesque, 1810b:20 (Sicily).

Thynnus rocheanus: Risso, 1826:417–419.

Auxis vulgaris Cuvier, 1831, *in* Cuvier and Valenciennes, 1831:139–146, pl. 216 (original description, Mediterranean); syntypes: MNHN A. 5808, A. 5815, not located by Bauchot and Blanc, 1961:375, Blanc and Bauchot, 1964:453 or Collette, 1966, but recently located in the MNHN collections during transfer of fishes to the new storage building.

Auxis thynnoides Bleeker, 1855:301 (original description, Ternate, Indonesia); holotype: RMNH 6049 (see Boeseman, 1964:464–465, pl. 3 fig. 9). Jones 1958:192–193, fig. 2 (India). Matsumoto, 1960a:

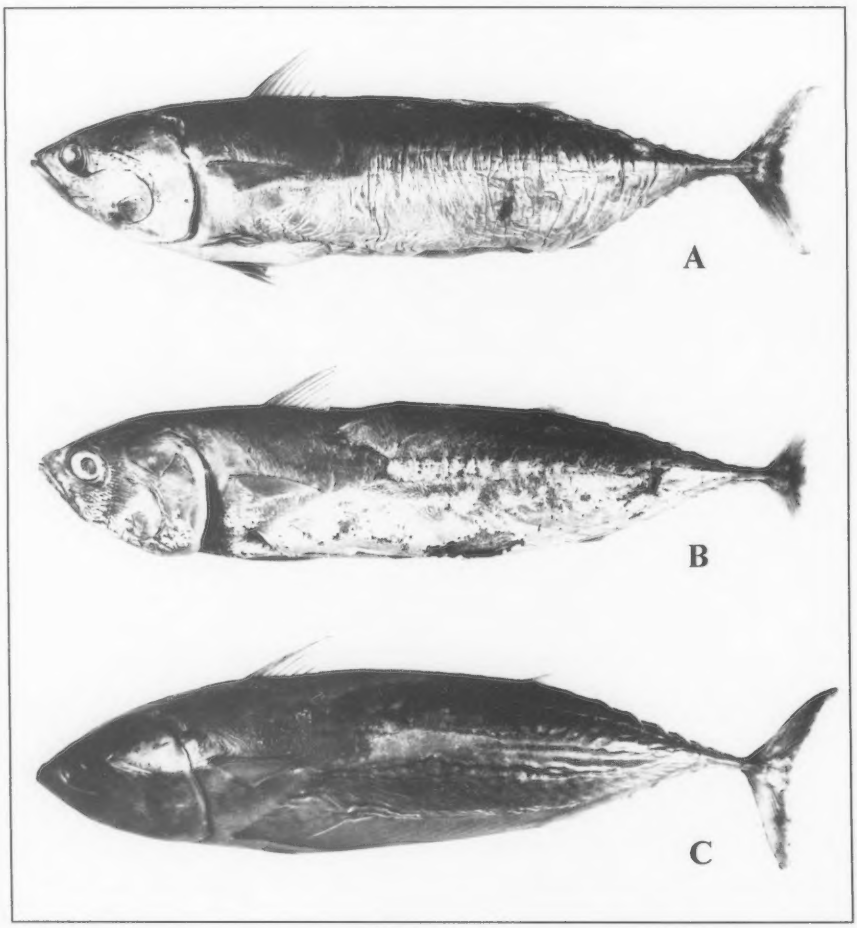

Figure 13

Type specimens of *Auxis rochei*. (**A**) Holotype of *Scomber rochei* Risso, 1810 and lectotype of *Auxis vulgaris* Cuvier, 1831; MNHN A.5808; 395 mm FL; Mediterranean Sea, Nice. (**B**) Holotype of *Auxis ramsayi* Castelnau, 1879; MNHN A.1241; 290 mm FL; Australia, Sydney. (**C**) Holotype of *Auxis rochei eudorax* n. ssp.; LACM 6712-1; 330 mm FL; California, 23 Fathom Bank.

173–174, fig. 1 (comparison of both species, Hawaii). Jones and Silas, 1961:378, fig. 4; 1963:1782–1786 (India). Jones, 1963:782–810 (species synopsis). Jones and Silas, 1964:23–24 (India).

Auxis Ramsayi Castelnau, 1879: 382 (original description, Port Jackson (Sydney), New South Wales, Australia); holotype MNHN A.1241.

Auxis rochei: Goode, 1880:808–810 and 1881:532–535 (first New England records). Fitch and Roedel, 1963:1331–1339, fig. 2 (generic review). Richards and Randall, 1967:245–247 (comparison with western Atlantic *A. thazard*). Chi and Yang 1972, (osteology, morphology, Taiwan). Richards and Klawe, 1972:67–68 (references to eggs and young). Gorbunova, 1974:50–52 (description, larvae, Pacific and Indian oceans, fig. 13). Rodríguez-Roda, 1980:169–176 (description, Spain). Uchida, 1981 (species synopsis). Collette and Nauen, 1983:29–30 (synonymy, description, distribution, fig.). Rodríguez-Roda, 1983 (age and growth, Spain). Richards, 1989:30–31 (description, larvae, western central Atlantic, figs. of 6 larvae, 3.5 mm NL to 39.0 mm SL).

Auxis thazard (*non* Lacepède, 1800): Dresslar and Fesler, 1889:434 (description, synonymy, in part), pl. 3 (USNM 25757, Rhode Island). Jordan and Evermann, 1896:867–868 (synonymy, in part). Fraser-Brunner, 1950: in part:152 (description; synonymy, in part). Rodríguez-Roda, 1966:279–291 (biology, eastern Atlantic).

Auxis maru Kishinouye, 1915:24 (original description, Japan); no type specimens known. Kishinouye, 1923:463464, pl. 31, fig. 56 (anatomy).

Diagnosis *Auxis rochei rochei* has fewer corselet scales, 5–24 (usually 6–19, Table 1), under the second dorsal-fin origin than *A. rochei eudorax,* 14–30 (usually 20–25).

Description Gill rakers 39–49, usually 41–47 in the Mediterranean, Gulf of Guinea, and Indo-West Pacific (Table 2); 39–46, usually 40–44 in the western Atlantic. The western Atlantic population has a narrower corselet (usually 6–9 scales wide under the second dorsal-fin origin compared with 8–19 in the eastern Atlantic and Indo-Pacific, Table 1) but appears best referred to as *A. r. rochei.* Corselet width under second dorsal-fin origin (Fig. 3) 2.0–10.0 mm, usually 3.0–7.0 mm, except in the western Atlantic where corselet width is only 1.0–4.0 mm, usually 1.5–3.5 mm. Dorsal scaleless area fails to reach pectoral-fin tip (Fig. 1) by up to 23.0 mm (Fig. 5); usually 3.0–17.0 mm in the Mediterranean, Gulf of Guinea, and Indo-West Pacific; may extend a little anterior to the pectoral-fin tip in the western Atlantic (Fig. 8).

Types

Scomber rochei Risso, 1810. Holotype MNHN A.5808 (395 mm FL), Mediterranean, Nice. Pectoral fin 50.1 mm; anterior extent of dorsal scaleless area extends 10.3 mm posterior to tip of pectoral fin; width of corselet under second dorsal-fin origin 3.7 mm; 12 scales in corselet under second dorsal-fin origin; gill rakers 9 + 33 = 42. Fig. 13A.

Auxis vulgaris Cuvier, 1831. Lectotype MNHN A.5808, herein selected. This specimen is also the holotype of *A. rochei*; thus *A. vulgaris* is an objective synonym of *A. rochei.*

Auxis thynnoides Bleeker, 1855. Holotype RMNH 6049 (260 mm FL), Indonesia, Ternate; C.F. Goldman. Pectoral fin broken, 27.2+ mm; dorsal scaleless area extends does not reach tip of pectoral fin; 5 scales in corselet under second dorsal-fin origin; gill rakers 11 + 36 = 47. Photograph of holotype in Boeseman (1964, pl. 3, fig. 9).

Auxis Ramsayi Castelnau, 1879. Holotype MNHN A.1241 (290 mm FL), Australia, New South Wales, Sydney. Pectoral fin 34.7 mm; anterior extent of dorsal scaleless area 12.7 mm posterior to tip of pectoral fin; width of corselet under second dorsal-fin origin 5.7 mm; 15 scales in corselet under second dorsal-fin origin; gill rakers 10 + 33 = 43. Fig. 13B.

Material examined 261 specimens (58.7–443 mm FL) from 102 collections.

Western Atlantic 37 specimens (96.4–442 mm FL) from 21 collections.

ROM 22066 (1, 292); off Nova Scotia, 41°06'N, 64°12'W; Jul 1955; Atlantic Bio Station. ROM 25064 (1, 350); Canada, Grand Bank; Aug 1967; E.O. Grandy. MCZ 39682 (1, 315); MA, Barnstable trap; 1 Aug 1954; F. Mather. USNM 35136 (1, 332); MA, Woods Hole; S.F. Baird. USNM 105002 (1, 285); MA, Woods Hole; 3 Jul 1936; H.M. Smith. ANSP 11335 (1, 283); RI, Newport; S. Powell. USNM 43717 (4, 322–340); RI, Newport; USFC. MCZ 26483 (1, 350); RI, Block I.; A. Agassiz. MCZ 40897 (1, 310); 20 mi S by E of No Man's Land; 30 Sep 1935; F.K. Schwomen. MCZ 123011 (1, 340); 40°05'N, 70°05'W; 29 Jun 1952; MV *Blue Dolphin.* USNM 50546 (1, 335); RI, off Block I.; H.C. Johnson. USNM 25973 (6, 420–442); RI, Newport; S.F. Baird. ANSP 119968 (1, 335); NJ, 29 mi ESE of Monasquain Inlet; 25 Jun 1966. ANSP 91791 (1, 340); NJ, Ventnor; 1946; C.B. Atkinson. USNM 127147 (9, 304–343); NJ. USNM 76694 (1, 324); MD, Ocean City; B.A. Bean. AMNH 3686 (1, 252); NC, Cape Lookout; summer 1910; R.J. Coles. USNM 325227 (1, 447); NC, Oregon Inlet. UF 38840 (1, 309); FL, Key Largo; A. Pflueger. USNM 325229 (1, 302); Florida; 20 Feb 1968. TU 6922 (1, 96.4); Gulf of Mexico, 28°27'N, 89°25'W; 9 Aug 1952; RV *Oregon,* R.D. Suttkus 2333.

Mediterranean 43 specimens (106–443 mm FL) from 22 collections.

USNM 266916 (1, 218); Israel, Haifa; 7 Jul 1960. HUJ 17073 (3, 318–328), Israel, purchased in Jaffa market; 17

June 1993; D. Golani. HUJ 17826 (1, 300); Haifa Bay; 8 Feb 1995; D. Golani. USNM 324234 (4, 134–147); Lebanon, St. George Bay; 10 Aug 1964; C. George. USNM 214659 (10, 119–155); Lebanon, St. George Bay; 28 Jul 1965; C. George. BMNH 1967.2.272–274 (3, 106–122); Lebanon, Antelias; C. George. NMW 14534 (1, 405); Yugoslavia, Fiume; 1881–1882; Steindachner. NMW 14531 (1, 443); Italy, Trieste; 12 Jun 1907; Steindachner. NMW 14532 (1, 408); Yugoslavia, Fiume; 1882; Steindachner. NMW 14533 (1, 399); Yugoslavia, Fiume; 1882; Steindachner. MNHN A.5808 (1, 395); Nice; Laurillard; holotype of *Auxis rochei* Risso. NMW 14537 (1, 335); France, Nizza; 1889. NMW 14538 (1, 395); France, Nizza; 1881. NMW 14527 (2, 297–303); Sicily; 9 Apr 1837. NMW 14536 (2, 149–228); France, Nizza; 1884.I.100; Steindachner. NMW 14535 (2, 108–113); France, Nizza; 1883; Steindachner. NMW 14551 (1, 435); Lissabon Dez; 1864; Steindachner. LACM 6707-1 (3, 377–410); Mediterranean Sea. MNHN A.5815 (1, 393); eastern Mediterrranean; Bory St. Vincent; paralectotype of *Auxis vulgaris* Cuvier. MCZ 58517 (1, 235); Straits of Messina; 10 Nov 1959; G. Arena. AMNH 5041 (1, 395); Italy, Naples; received Jun 1913. USNM 198207 (1, 362); Italy, Genoa; 1964; E. Tortonese.

Eastern Atlantic 69 specimens (212–399 mm FL) from 10 collections.

BMNH 1983.9.8.203 (1, 287); Azore Is.; Stonehouse. ISH 173/64 (2, 345–390); Cape Verde Is., 16°05'N, 22°45'W; RV *Walther Herwig* 81/64; 14 Mar 1964. USNM 325217 (15, 343–399); Gulf of Guinea; 15 Oct 1967; MV *Caribbean*, set 1. USNM 325955 (1, 212); Ghana; 5 Oct 1967. BMNH 1932.2.27.17 (1, 297); Ghana, Accra; Irvine. USNM 189004 (1, 279); Liberia; 27–29 Oct 1952; G.C. Miller 1789. USNM 218954 (1, 330); Angola, Baia Farta, 12°36'S, 13°12'E; 5 Apr 1968; RV *Undaunted* 68-279. USNM 325218 (32, 278–307); Angola, Benguela, 12°36'N, 13°12'E; 29 Mar 1968; RV *Undaunted* 68-273. USNM 325219 (14, 271–334); Angola, Baia Farta, 12°36'S, 13°12'E; 5 Apr 1968; RV *Undaunted* 68-279. BMNH 1868.6.15.11 (1, 390); St. Helena; Melliss.

Indian Ocean 9 specimens (175–273 mm FL) from 6 collections.

CMFRI uncat (1, 273); India, Cochin Harbor; 2 Oct 1979. CMFRI uncat (2, 198–267); India. CMFRI uncat (1, 198); India, Cochin Harbor; Oct 1979. CMFRI uncat (1, 175); India, Vellayil, Calicut; 31 Aug 1979. CMFRI uncat (1, 181); India, Cochin Harbor; 11 Sep 1979. USNM 215024 (3, 241–243); Ceylon; P.C. Heemstra.

Western Pacific 90 specimens (58.7–335 mm FL) from 41 collections.

MCZ 32422 (3, 295); Russia, Vladivostok market, Peter-the-Great Bay; 1925; Pacific Fisheries Institute. CAS SU 24121 (1, 262); Japan, Tokyo; 21 Oct 1932; D.S. Jordan. CAS SU 11763 (1, 213); Japan; 1895; K. Otaki. CAS SU 23788 (1, 235); Japan, Etcha; 1922; Ishikawa and Wakiya. MCZ 58514 (1, 173); Japan, near Tokyo; T. Abe. MCZ 58516 (1, 167); Japan, near Tokyo; T. Abe. AMNH 34877 (1, 240); Japan, Tokyo market; 31 Oct 1922; D.S. Jordan. AMNH 26893 (1, 216); Japan, Misaki; 1922; K. Aoki. AMNH 13025 (1, 250); Japan, Kyoto market; 1922; D.S. Jordan. UMMZ 142722 (1, 252); Japan, Tokyo market; 31 Oct 1922; D.S. Jordan. ZUMT 16380 (1, 270); Japan, Miyagi Pref., off Ishinomaki City; 10 Sep 1925. ZUMT 13758 (1, 311); Japan, Hokkaido, Muroran City; Sep 1924. ZUMT 20200 (1, 237); Japan, Wakayama Pref.; Jan 1920. ZUMT 46643 (1, 331); Japan, Niigata Pref.; Aug 1923. ZUMT 51365 (1, 250); Japan, Fukuoka fish market; 10 Dec 1959. ZUMT 41208 (1, 214), 41213 (1, 215), 41220-24 (5, 201–219), 41228 (1, 210), 41249-57 (9, 200–225), and 41282-84 (3, 206–216); Japan, Toyama Pref., Namerikawa. ZUMT 54922 (1, 214); Japan, Shizuoka Pref., Izu Peninsula; 12 Sep 1981; M. Aizawa. ZUMT 50407 (1, 243); Japan, Nagasaki Pref.; Motoura, Ikitsuki I.; 25 Oct 1953. CAS SU 49371 (1, 270); Taiwan; Chu. CAS SU 14524 (3, 230–240); Philippine Is., Luzon; 1934; Herre. CAS SU 28284 (1, 235); Philippine Is., Culion; Apr 1931; Herre. USNM 325236 (5, 227–233); Philippine Is., N. Palawan; 17 Sep 1963; I. Ronquillo. USNM 325233 (3, 217–236); Philippine Is., Almahon Bato; 17 Sep 1963. USNM 326677 (1, 209); Philippine Is., Manila Bay; 27 May 1962. USNM 339044 (6, 256–285); Philippine Is., Manila markets; 1–10 Oct 1995; B.B. Collette. LACM 45781-1 (17, 58.7–93.8); Philippine Is., Luzon, Batangas Bay, Bauan; 27 Mar 1949; M.A. Sabalo and Leonicio. SIO 75–149 (1, 156); 9°51.4'N, 117°32.5'W; 16 Nov 1970; F. Williams. SIO 61–736 (4, 173–179); Gulf of Thailand, 41 mi from Ban Laehn Pho, Pattani; 16 Nov 1960; RV *Stranger*. AMNH 15865 (2, 270–275); Java, Batavia; 5 Dec 1941; Inst. Zoevisch. RMNH 6049 (1, 260), East Indies, Ternate; C.F. Goldman; holotype of *Auxis thynnoides* Bleeker. MNHN A.1241 (1, 290); Australia, New South Wales, Sydney; F. Castelnau; holotype of *Auxis ramsayi*. AMS IB 4015 (1, 335); Australia, New South Wales, Sydney; G.P. Whitley. AMS IB 3227 (1, 325); Australia, New South Wales, Newcastle district; A. D'Ombrain. AMS IB 3535 (1, 318); Australia, New South Wales, off Port Stephens; A. D'Ombrain. AMS IB 1804 (1, 300); Australia, New South Wales, Shoal Bay. AMS I 15313 (1, 284); Australia, New South Wales, Shoal Harbor.

Central Pacific 13 specimens (50.5–283 mm FL) from 2 collections.

BPBM 27044 (6, 260–283); Hawaii, Cape Kaea, Lanai; 30 Nov 1957; RV *John R. Manning*, cr. 38. LACM 45779-1 (7, 50.5–59.2); Hawaiian Is., RV *Townsend Cromwell*, cr. 43, sta. 30; 17 May 1969.

Auxis rochei eudorax Collette and Aadland, new subspecies

Fig. 13C

Diagnosis *Auxis rochei eudorax* has more corselet scales under the second dorsal-fin origin (Table 1), 14–30 (usually 20–25) than *A. rochei rochei*, 5–24 (usually 6–19).

Description Gill rakers 43–48, usually 44–47 (Table 2). Corselet width under second dorsal-fin origin 5.0–11.0 mm, usually 7.0–10.0 mm (Fig. 3).

Etymology We use the name that Fitch and Roedel used in their manuscript, *eudorax* from the Greek

eu (well) and *dora* (hide) in reference to the wide or well-developed corselet. Carl L. Hubbs suggested this name in a memo dated 1 Feb 1951 to W.I. Follett, concerning an edition of their California fish list, with copies to Fitch and Roedel.

Material examined 30 specimens (300–365 mm FL) from 17 collections.

Holotype LACM 6712-1 (330 mm FL); CA, 23 Fathom Bank; 13 Jan 1955; R.D. Collyer; field number SSY 1-2. Pectoral fin 41.7 mm; anterior extent of dorsal scaleless area extends 8.1 mm posterior to tip of pectoral fin; width of corselet under second dorsal-fin origin 10.2 mm; 25 scales in corselet under second dorsal-fin origin; gill rakers 11 + 36 = 47. See Fig. 13C.

Paratypes from the eastern Pacific 29 specimens (300–365 mm FL) from 17 collections.

LACM 6711-5 (1, 350); CA, Balboa Pier; 17 Sep 1960; J.P. Reed. LACM 6711-6 (1, 312); CA, off Newport Beach; 13 Dec 1961; A. Gronsky. LACM 6711-3 (1, 338); CA, outside of Newport Beach; 13 Dec 1961; A. Gronsky. LACM 6711-4 (1, 322); CA, off San Clemente; 15 Sep 1960. LACM 6711-1 (1, 355); CA, Los Coronados Is.; 4 Nov 1957; MV *Lo-An*. LACM 34069-2 (1, 318); CA, between Oceanside and San Clemente; 30 Sep 1972. CAS 56944 (1, 363); CA, between Half Moon and San Francisco bays; 29 Oct 1984; MV *Aries*. CAS 54921 (1, 335); CA, San Luis Obispo Co., 30 mi N of Morro Rock, 7 Sep 1983; MV *Mary Beth*. LACM 6711-11 (1, 340); California; Jun–Jul 1951; MV *Courageous*. LACM 6712-2 (6, 300–325); CA, 23 Fathom Bank; 13 Jan 1955; R.D. Collyer; field number SSY 1-2. LACM 6711-10 (1, 316); California. LACM 6711-7 (3, 320–340); Baja Calif., Cape San Lucas; May 1950; MV *Nancy Rose*. LACM 39621-1 (1, 308); Mexico, Pta. Pequera, San Juanico; 24 Nov 1953; J.E. Fitch. CAS 56978 (1, 365); Baja California, below Holcombe Pt.; 25 Jul 1958; Walker and Connolly. LACM 6708-2 (3, 313–338); Gulf of California, 450 Fathom Bank; 24 Mar 1950; MV *Nancy Rose*. LACM 6709-1 (3, 309–331); Panama Bay, N of Isla Chepillo, 8°58'N, 79°10'W; 27 Feb 1954; MV *Mayflower*. ANSP 89082 (2, 340–343); Galapagos, James I., Sullivan Bay; 4 Jul 1941; Fifth Vanderbilt Expedition.

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Age, growth, and mortality of bonefish, *Albula vulpes*, from the waters of the Florida Keys

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Abstract.—We examined 528 bonefish ranging from 21 to 702 mm FL collected in South Florida waters from 1989 to 1995. Ages of 451 bonefish ranging from 228 to 702 mm FL were estimated from thin-sectioned otoliths (sagittae). Examination of OTC-marked otoliths from five fish held in a pond in the Florida Keys for periods ranging from 14 to 29 months suggested that a single annulus was formed each year. Marginal-increment analysis also showed that a single annulus was formed each year during March–June. Bonefish reach a maximum age of at least 19 years. Growth of the bonefish in our study was rapid until an age of about six years and then slowed considerably. The von Bertalanffy growth equation for females was $FL=680.9(1-e^{(-0.279(Age+0.934))})$ and for males was $FL=670.7(1-e^{(-0.242(Age+1.318))})$. The overall growth models for males and females were significantly different, but estimates of individual growth parameters L_∞, K, and t_0 were not. Predicted lengths of females were greater than those of males for all ages greater than 1 year. Catch-curve estimates of instantaneous rates of total mortality (Z) were 0.21 (95% confidence interval 0.167–0.303) for females and 0.25 (95% confidence interval 0.098–0.406) for males. Empirically derived estimates of natural mortality were similar to total mortality estimates, suggesting that fishing mortality is low.

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Bonefish, *Albula vulpes*, are moderate-size elopomorph fish that frequent coastal and inshore waters of tropical seas worldwide. In the western Atlantic, bonefish regularly occur in the Florida Keys, the Bahama Islands, and throughout the Caribbean Sea (Hildebrand, 1963). In many areas of the species' range, including the waters off the Florida Keys, bonefish are the basis of economically important recreational fisheries. Bonefish are renowned by anglers for their wariness and fighting abilities and are often caught in water as shallow as 0.3 m. In the Florida Keys, fishing for bonefish is a year-round activity and provides an important source of income for professional fishing guides. The commercial sale of bonefish in Florida is prohibited; the limits placed upon the recreational fishery for bonefish are a bag limit of one fish per angler per day and a minimum fish size of 457 mm total length. Bonefish are not considered a food fish in Florida, and most bonefish caught are released.

Bonefish life history has not been adequately described. Bruger (1974) described the age and growth of bonefish from an examination of scales of 205 bonefish from South Florida waters. He estimated the age of the oldest bonefish in his study to be 12 years and suggested that greater ages may be attained. His attempt to validate annulus formation on scales using the marginal-increment technique was inconclusive, perhaps because annulus formation in scales often occurs over a prolonged period and because annuli are often closely spaced in older fish, making validation of scale-derived ages by the marginal-increment technique difficult (Lowerre-Barbieri et al., 1994). In addition, Bruger's sample sizes for many months were small.

Since Bruger's work, studies on a variety of species have shown that scales are not reliable for ageing long-lived fishes and that scale-derived age estimates are typically lower than validated estimates derived from sectioned otoliths (Beamish and McFarlane, 1983; Casselman, 1983; Lowerre-Barbieri et al., 1994). Ageing of bonefish with a validated method is needed to assess Bruger's estimates of longevity. In addition, sex-specific differences in growth rates have not been evaluated and growth-model parameters have not been estimated for Florida bonefish. The only published growth-model parameters for bonefish are those by Morales-Nin (1994), who used length-frequency analyses to estimate von Bertalanffy growth parameters for a small sample of bonefish from Mexico's Pacific coast. In this article, we describe the age and

growth of bonefish from the waters off the Florida Keys and estimate mortality rates from a sample of fish whose ages were determined from an examination of sectioned otoliths.

Methods

We examined 528 bonefish collected from South Florida waters from February 1989 to April 1995. Most of these bonefish were caught with hook-and-line gear either by biologists or by a single professional bonefish guide and his anglers from waters off the Florida Keys and in Florida and Biscayne Bays. Five bonefish caught with hook-and-line gear were obtained from taxidermists in Fort Lauderdale and five others from tournaments in waters off the Keys. Supplemental collections of small bonefish (<425 mm) were made with various-size seines and gill nets in waters off the Keys. We collected young-of-the-year (YOY) bonefish using 21.4-m seines constructed with 6.35-mm mesh. These collections were made from shallow (<1 m) sand- and grass-bottom areas on the ocean (Florida Straits) side of Key West, Bahia Honda Key, and Lower Matecumbe Key and from the Indian River Lagoon on Florida's Atlantic coast.

Standard length (SL), fork length (FL), and total length (TL) were measured to the nearest millimeter (mm) and fish were weighed to the nearest gram. All lengths reported are fork lengths. Otoliths (sagittae) were removed, cleaned with bleach (5.25% sodium hypochlorite), and rinsed first in water and then in 95% ethanol. Otoliths were stored dry until sectioned. Sex of all fish, except that of YOY (age 0), was recorded and confirmed histologically.

The left sagitta was usually used for age estimation; however, in cases where the left otolith was broken, lost, or damaged during processing, the right otolith was substituted. We prepared most otoliths by cutting three or four thin sections approximately 0.5 mm thick, one of which was through the otolith core, using a Buehler Isomet low-speed saw with a diamond blade. Sections were then mounted on a microscope slide with Histomount. Initially, we prepared some otoliths for age estimation by embedding them in Spurr, a high-density plastic medium (Secor et al., 1992). A 1- to 2-mm thick transverse section containing the otolith core was cut. The section was mounted on a microscope slide with thermoplastic glue (CrystalBond 509 adhesive) and polished with wet/dry sandpaper (grit sizes ranging from 220 to 2,000 grits per sheet) until annuli were visible. Sections were then polished on a Buehler polishing cloth with 0.05-μ gamma alumina powder to remove scratches. There was no consistent difference in the quality of either preparation technique. Mounting the sections in Histomount took less time than embedding them in Spurr; therefore, this technique was adopted as our standard protocol.

Annuli were counted three times by each of two independent readers who used a dissection microscope equipped with reflected light at magnifications of 8–25×. After the readers completed counting annuli on all the otoliths, we re-examined the otoliths for which different counts had been given. Most disagreements in counts concerned the presence or absence of an annulus on the otolith's margin. We were usually able to reconcile these disagreements and to assign an age to the otolith. A few otoliths had irregular and poorly defined annuli (n=20, 4.2%); these were discarded from the analysis.

Measurements for marginal-increment analysis were made with a digital image-processing system along an axis extending from the otolith's core to the ventral proximal margin of the section (Fig. 1). We expressed the distance from the final annulus to the otolith's edge (marginal increment) as a percentage of the distance between the last two annuli formed on the otolith. For all bonefish, the distance between the otolith core and the first annulus (r_1) was typically much greater than the distance between the first and second annuli (r_2–r_1). For this reason, we divided the distance between the first and second annuli by the distance between the otolith's core and the first annulus for each otolith measured and then calculated the mean of this number for the entire sample,

$$\frac{\sum_{i=1}^{n}\left((r_2 - r_1)/r_1\right)_i}{n} = 0.406 \qquad (\mathrm{SE} = 0.0081).$$

We then estimated the expected distance between the first and second annulus for each age-1 bonefish otolith as a function of the distance between the otolith's core and the first annulus. The percent marginal increment for age-1 fish was then calculated as $(MI/(0.406 \times r_1))\cdot 100$, where MI = the marginal increment. We then plotted the median percent marginal increment as a function of capture month for the 36-month period during which we made regular monthly bonefish collections. We also plotted marginal increments for individual age classes 4–9 for all study years pooled. Our monthly sample sizes for other individual age classes were insufficient for marginal-increment analysis.

Bonefish were captured with hook-and-line gear from the waters off the Florida Keys for age-valida-

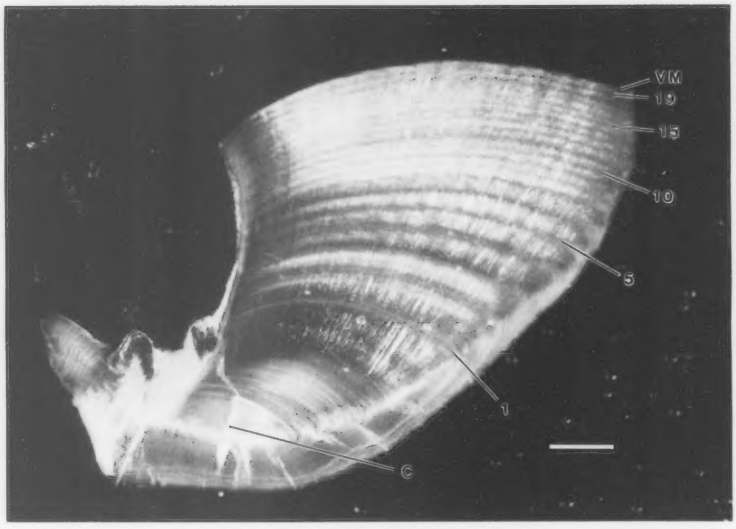

Figure 1

Transverse section from a 19-year-old (641-mm-FL) bonefish, *Albula vulpes*, otolith viewed with reflected light showing the annuli counted for age estimation. Measurements for marginal-increment analysis were made along an axis extending from the otolith core (c) to the ventral margin (vm) of the section. Scale bar = 1 mm.

tion experiments (Table 1). After capture, fish were measured for fork length and tagged with dart-type tags. Bonefish were then injected with Liquamycin LA-200 (200-mg oxytetracycline [OTC]/mL) in the dorsal musculature at a dosage of 100-mg OTC per kg fish weight. Fish weight was estimated with a length-weight regression. Bonefish were then transported to a 33.5-m by 5.5-m by 0.75-m deep pond at the Keys Marine Laboratory in Long Key, where they were held for 14 to 29 months. Water at ambient temperatures was pumped continuously from Florida Bay through the pond. Fish were fed at least three times a week with as much frozen fish or shrimp as they would consume. Sections from OTC-marked otoliths were examined with a compound microscope (40–100×) equipped with ultraviolet light so that the fluorescent OTC marks could be detected.

The von Bertalanffy (1957) growth equation $FL_t = L_\infty(1-e^{-K(t-t_0)})$ was fitted to observed age-length data with nonlinear regression procedures. Likelihood-

Table 1

Data for oxytetracycline (OTC)-injected bonefish, *Albula vulpes*. Otolith measurements were made along an axis extending from the otolith core to the OTC mark, annuli, and ventral margin of the section (Fig. 1). Measurements were made to the annulus at or just before the OTC mark and all subsequent annuli.

Injected		Sacrificed				Distance from core (mm)				
Date	Fork length (mm)	Date	Fork length (mm)	Months held	Age (years)	OTC mark	Annulus	Annulus	Annulus	Otolith edge
Nov 91	546	Oct 93	583	24	5	4.85	4.89	5.44		5.81
April 92	660	Nov 93	661	20	18	7.61	7.57	7.73		7.94
Oct 92	465	Nov 93	511	14	4	5.34	5.39			5.98
Oct 92	360	March 94	465	18	4	4.82	4.84	5.68		5.77
Dec 91	—	April 94	645	29	15	6.83	6.84	7.10	7.28	7.31

ratio tests were used to compare parameter estimates for males and females (Kimura, 1980; Cerrato, 1990). We used the outlier detection methods described by Sokal and Rohlf (1995) to test the significance of two perceived outliers from the age-length and otolith weight-age relations. Dixon's test statistic for outliers was used for sample sizes ≤25, and Grubb's test statistic for outliers was used for larger sample sizes. Outliers were considered significant at the $P<0.05$ significance level. Because we could not sex YOY bonefish, they were not included in growth models, but they were included in length-length regressions and pooled length-weight regressions. Sex-specific length-weight regressions were calculated by linear regression of $\log_{10}$-transformed data, and we compared the slopes and elevations using a t-test (Zar, 1984).

We used a catch curve to estimate the instantaneous total mortality rate (Z) from age-frequency data (Robson and Chapman, 1961). The age of full recruitment to the fishery for the catch-curve analysis was assumed to be 5 years, and year classes represented by fewer than five individuals were eliminated from the analysis. We estimated the instantaneous rate of natural mortality (M) using Pauly's (1980) formula $\ln M = -0.0152 - 0.0279\ln L_\infty + 0.6543\ln K + 0.463\ln T$, where L_∞ and K are parameters from the von Bertalanffy growth equation, and T is the average annual surface temperature. An average annual temperature of 25.9°C (SD=0.13) was calculated from daily temperature measurements made from 1992 to 1994 at the Keys Marine Laboratory's water intake pump in Florida Bay. Pauly (1983) suggested that for schooling species, such as bonefish, the estimate of natural mortality derived from the above equation should be reduced by 20%. We used Pauly's formula and the 20% correction to suggest a possible range of values for natural mortality.

Undamaged otoliths were weighed to the nearest 0.01 mg in order to evaluate the use of otolith weight as a predictor of age. If both left and right otolith weights were available for an individual fish, the mean of the two weights was calculated. Sex-specific linear regressions were fitted to $\log_{10}$-transformed otolith weight and age data, and we compared the slopes and elevations of the regressions using a t-test (Zar, 1984).

Results

The 528 bonefish we examined ranged from 21 to 702 mm in length; 56 (10.6%) of these fish were YOY (21–116 mm). Fish caught on hook-and-line gear ranged in length from 228 to 702 mm (median=591 mm, interquartile range=111 mm, n=452) and most (80%) were from 500 to 700 mm (Fig. 2). Among all bonefish that we sexed, females ranged from 228 to 702 mm in length (median=601 mm, interquartile range=110 mm, n=274) and males ranged from 290 to 700 mm (median=566 mm, interquartile range=146 mm, n=192). The size-frequency distributions of males and females were significantly different (Kolmogorov-Smirnov two-sample test, D=0.231, $P<0.001$); females were significantly larger than males (Mann-Whitney U-test, $P<0.001$). Females were also more abundant than males. In our sample there were 192 males and 274 females, and the sex ratio was significantly different from 1:1 (χ^2=14.43, df=1, $P<0.001$).

Neither slopes (t-test, df=453, t=0.474, P=0.318) nor elevations (t-test, df=454, t=0.084, P=0.467) of the length-weight regressions for male and female bonefish were significantly different. The pooled length-weight equation for sexed and unsexed fish and the relations between SL, FL, and TL are presented in Table 2.

Bonefish otoliths when viewed with reflected light have clear and easily counted narrow, opaque (bright) annuli that alternate with broad translucent (dark) zones (Fig. 1). Proceeding from the otolith's core towards the otolith's proximal margin, these translucent zones become increasingly opaque in appearance as the otolith grows. In the portion of the otolith

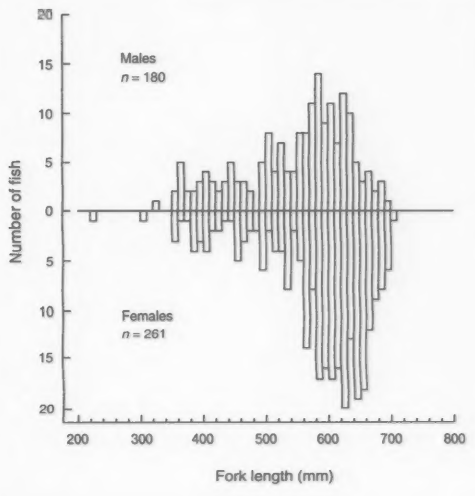

Figure 2
Length-frequency distributions for Florida Keys bonefish, *Albula vulpes*, caught with hook-and-line gear.

Table 2

Length-length, length-weight, and otolith weight-age regressions for bonefish, *Albula vulpes*, from the waters of the Florida Keys. TL = total length (mm), FL = fork length (mm), SL = standard length (mm), WT = weight (g), OWT = otolith weight (g), and AGE = age in years. Sample fork-length range for all length-length and length-weight regressions was 21–702 mm. Age range for the otolith weight-age regression was 1–19 years. Values in parentheses are standard errors.

			$Y = a+bX$		
Y	X	n	a (1 SE)	b (1SE)	r^2
FL	SL	521	4.5538 (1.0819)	1.0284 (0.0021)	0.998
FL	TL	516	–5.3384 (1.0297)	0.8652 (0.0017)	0.998
SL	FL	521	–3.3737 (1.0584)	0.9703 (0.0020)	0.998
SL	TL	516	–8.5152 (1.4894)	0.8394 (0.0024)	0.996
TL	FL	516	7.2580 (1.1770)	1.1537 (0.0022)	0.998
TL	SL	516	12.5401 (1.7404)	1.1864 (0.0034)	0.996
$\log_{10}$WT	$\log_{10}$FL	518	–5.3240 (0.0142)	3.1871 (0.0054)	0.999
$\log_{10}$OWT	$\log_{10}$AGE	427	–0.7161 (0.0107)	0.6489 (0.0133)	0.849

formed after about age 4, the dark translucent zones are narrow and only apparent in the region immediately adjacent to the annuli. The broad opaque zones in the outer portions of the otolith section are separate and distinct from the narrow opaque annuli, which are still visible at higher magnifications (30–50×) within the translucent zones in older fish, especially along the ventral ridge of the sulcus acusticus and the ventral margin of the otolith section.

We examined OTC-marked otoliths from five bonefish ranging from 465 to 661 mm in length and from 4 to 18 years in age (Table 1). All otoliths showed the expected pattern of otolith growth; one annulus had been formed per year. Marginal-increment analysis of otoliths also suggested that one annulus had been formed during March–June each year (Fig. 3). Median marginal increments had a consistent seasonal minimum during April–June and a maximum in October–February from 1992 to 1994. When median marginal increments were plotted for individual age classes 4–9, a similar pattern was seen (Fig. 4).

Of 471 otoliths processed for age estimation, only 20 (4.2%) were rejected because of disagreements among readings. The length-frequency distribution of fish whose otoliths were rejected because they were unsuitable for age estimation was not significantly different from that of all fish whose otoliths were examined (Kolmogorov-Smirnov two-sample test, D=0.234, P=0.22). The oldest bonefish examined were a 650-mm female estimated to be 19 years old and a 641-mm male also estimated to be 19 years old (Table 3). Bonefish growth was rapid until an age of about 6 years and then slowed considerably (Fig. 5). Results of likelihood-ratio tests showed a significant difference in the overall von Bertalanffy growth models for males and females (χ^2=26.15, df=3, P<0.001, Table 4). Estimates of L_∞ (χ^2=0.406, df=1, P=0.52), K (χ^2=1.54, df=1, P=0.21), and t_0 (χ^2=1.28, df=1, P=0.26) were not significantly different between sexes. Lengths at age predicted by the von Bertalanffy equation agreed with the observed lengths of both female and male bonefish (Fig. 5). Predicted lengths at age of females were greater than those of males for all ages greater than 1 year, and observed lengths at age of females were greater than those of males for all ages except 1 and 18 (Table 3). The age-frequency distributions of males and females were significantly different (Kolmogorov-Smirnov two-sample test, D=0.265, P<0.001); females (median age=7 yr, interquartile range=4 yr, n=262) in our sample were significantly older than males (median age=6 yr, interquartile range=4 yr, n=181; Mann-Whitney U-test,

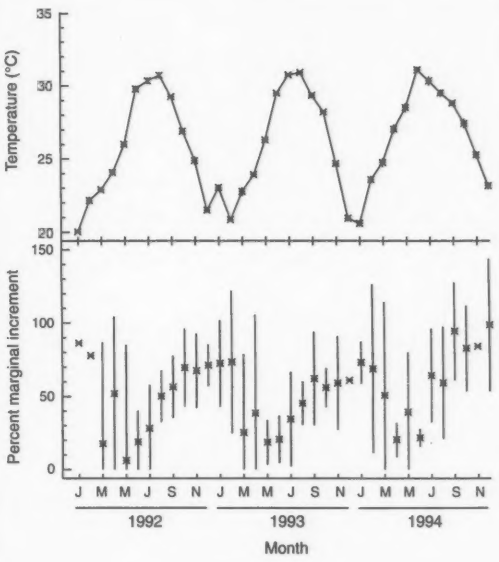

Figure 3

Mean monthly water temperatures (°C) calculated from daily temperature measurements at the water intake pump in Florida Bay adjacent to the Keys Marine Laboratory, and monthly median percent marginal increment and interquartile range for bonefish, *Albula vulpes*, otoliths.

P=0.012). Most bonefish (86%) in our sample that were caught with hook-and-line gear were from 3 to 10 years old (Fig. 6). On the basis of visual inspection of the age-frequency distributions, bonefish were not fully recruited to the fishery until an age of about 5 years.

The instantaneous rate of total mortality (Z) estimated by our catch-curve analysis was 0.25 (95% confidence interval 0.098–0.406, r^2=0.805, n=7, P<0.001) for males and 0.21 (95% confidence interval 0.167–0.303, r^2=0.922, n=9, P<0.001) for females. The instantaneous rate of natural mortality (M) estimated with Pauly's formula was 0.29 for males and 0.31 for females. The 20% reduction of this estimate recommended by Pauly (1983) for schooling species suggests a range of 0.2–0.3 for natural mortality.

Otolith weight was significantly related to age (Fig. 7). The slopes (t-test, df=417, t=1.34, P=0.09) and intercepts (t-test, df=418, t=0.49, P=0.31) of the otolith weight-age equations for males and females were not significantly different (Table 2).

Two of the bonefish that we aged were exceptionally small for their estimated ages and the weights of their otoliths were exceptionally light. One was a 351-mm female that was 7 years old and the other was a 458-mm female that was 18 years old. These two fish were statistically significant outliers, and we excluded them from growth models, age-frequency distributions, and otolith weight-age regressions. Both fish were caught with hook-and-line gear on the ocean (Florida Straits) side of North Key Largo, and they were the smallest females examined with active vitellogenic ovaries.

Discussion

We obtained bonefish from a variety of fishery-dependent and fishery-independent sources, but all fish larger than 405 mm that we examined were caught with hook-and-line gear. The size-frequency distribution of the hook-and-line-caught fish in our sample is probably similar to that of the fish caught in the fishery. Most of the hook-and-line-caught fish we examined were killed without regard to size, but a few fish included in our analysis were received from private anglers, tournaments, and taxidermists, sources that were presumably biased towards larger fish. Bonefish were not fully recruited to the hook-and-line gear until they reached a length of 550–600 mm and an age of about 5 years. We assume that our sample was representative of the Keys bonefish population beyond this size and age, but it is possible that hook-and-line gear introduced unknown biases that affected our mortality rates and growth-parameter estimates. We have no basis to evaluate the extent of these potential biases.

Age-validation experiments with OTC-marked otoliths supported our hypothesis that bonefish otoliths formed annual marks, and marginal-increment analysis suggested that annuli formed during March–June. Although sample sizes were insufficient to reveal trends for some individual age classes, age classes 4–9 showed marginal-increment patterns consistent with our hypothesis that annuli formed during March–June. Annulus formation appears to take place shortly after the season of minimal water temperatures in the Keys (Fig. 3). Monthly mean temperatures in Florida Bay at the Keys Marine Laboratory's water intake pump varied seasonally from a low of about 21°C during mid-December–February to a high of about 31°C during June–September (Fig. 3). These temperatures were probably similar to those of typical Keys bonefish habitat, and indeed on several occasions we collected bonefish on the flats adjacent to the pump. It is possible that holding fish under captive conditions and an artificial feeding regime affected the periodicity of annulus formation. However, we saw no change in the appearance or widths of the alternating translucent

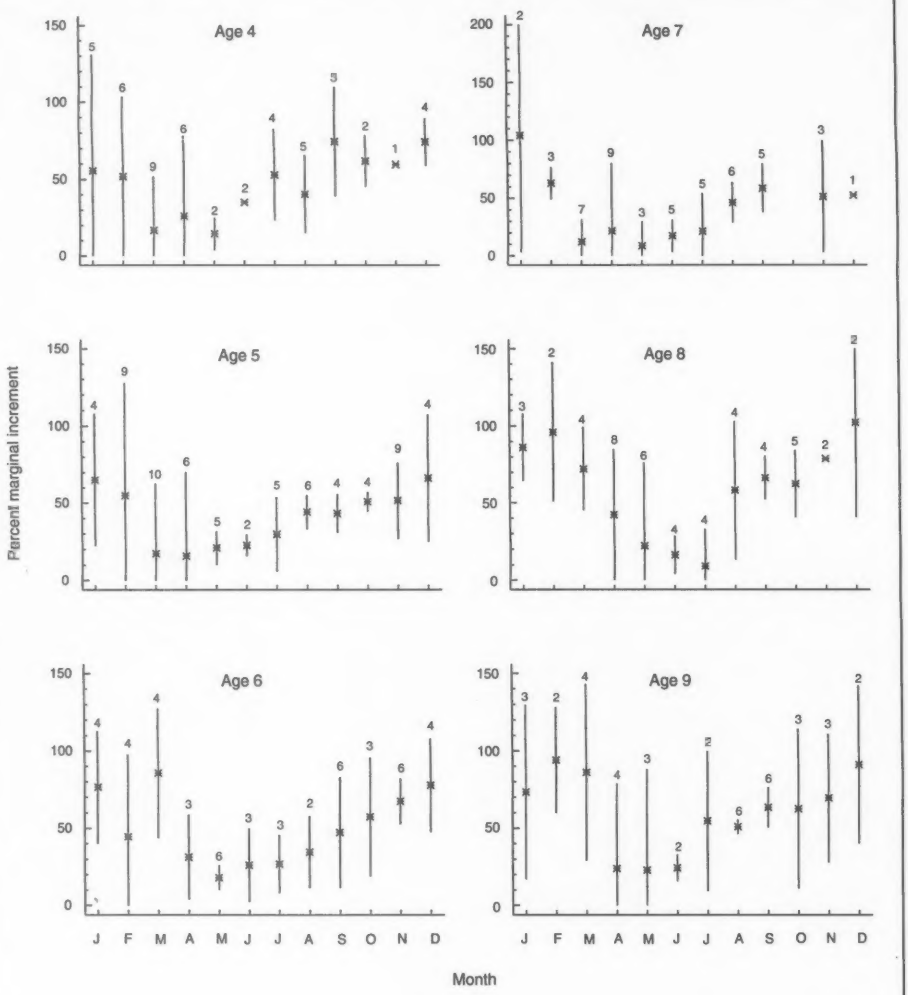

Figure 4

Monthly median percent marginal increment and interquartile range for bonefish otoliths for individual bonefish, *Albula vulpes,* age classes 4–9.

and opaque zones on otolith sections distal to the OTC mark to suggest that otolith growth had been fundamentally altered.

Our findings suggest that scales may not be suitable for ageing bonefish older than 6–9 years, the point at which our length-at-age data reached an asymptote. Scale-derived estimates of bonefish longevity by Bruger (1974) are lower than our otolith-derived estimate of 19 years. The oldest fish Bruger reported was estimated to be 12 years old, but he presented age-at-length data for only 140 bonefish ages 1–9. The number of fish in Bruger's sample declined quickly after age 6, and he apparently found only one fish older than age 9. In contrast, we found bonefish ages 3–9 to be abundant, and small numbers of fish were present in each age class from ages 10 to 19 yr (Fig. 6). The truncated age structure of Bruger's sample is probably an artifact of his ageing technique, but because we did not directly compare scale-derived and otolith-derived ages, we cannot rule out the possibility that Bruger's sample contained only one fish older than age 9.

Table 3

Average observed and predicted fork lengths (mm) for male and female bonefish, *Albula vulpes*, and average observed fork lengths for unsexed bonefish. Values in parentheses are standard error and sample size.

	Male		Female		Unsexed
Age (yr)	Average observed	Predicted	Average observed	Predicted	Average observed
1	320 (8.8; 7)	288	311 (13.4; 9)	284	
2	362 (4.7; 5)	370	374 (19.5; 8)	381	
3	401 (9.2; 19)	435	403 (10.9; 11)	454	399 (7.0; 2)
4	493 (11.6; 22)	486	499 (12.7; 27)	509	437 (37.0; 2)
5	531 (10.1; 33)	525	567 (8.1; 38)	551	538 (1)
6	559 (13.6; 20)	557	585 (7.2; 31)	583	608 (1)
7	588 (8.4; 17)	581	605 (6.3; 33)	606	597 (1)
8	619 (7.0; 19)	600	633 (4.2; 31)	625	635 (1)
9	608 (7.0; 17)	615	641 (7.4; 25)	638	
10	614 (7.6; 6)	627	651 (8.1; 16)	649	
11	618 (10.8; 7)	637	638 (25.0; 7)	657	
12	637 (17.0; 3)	644	672 (6.9; 5)	662	668 (1)
13	660 (1)	650	670 (29.0; 2)	667	
14		654	635 (18.0; 2)	670	
15	672 (1)	658	674 (13.6; 3)	673	
16		661	654 (3.0; 3)	675	
17	644 (1)	663	679 (5.7; 5)	676	
18	659 (22.0; 2)	664	642 (1.2; 3)	677	
19	641 (1)	666	650 (1)	678	

Table 4

Parameter estimates for the von Bertalanffy growth model for bonefish, *Albula vulpes*, collected from the waters of the Florida Keys. Values in parentheses are standard errors.

Sex	n	L_∞ (mm)	K	t_0	r^2
Males	181	670.7 (14.74)	0.242 (0.0256)	−1.318 (0.3205)	0.770
Females	260	680.9 (8.55)	0.279 (0.0195)	−0.934 (0.2031)	0.792

Although our growth models for male and female bonefish were significantly different, the differences were small. This is reflected in our findings that individual growth parameters were not significantly different, that the two growth curves appeared similar (Fig. 5), and that the maximum sizes attained by both sexes were similar. Observed lengths at age for females were larger than those for males in all but two age classes, which is consistent with the higher growth rates for females. The median length of the

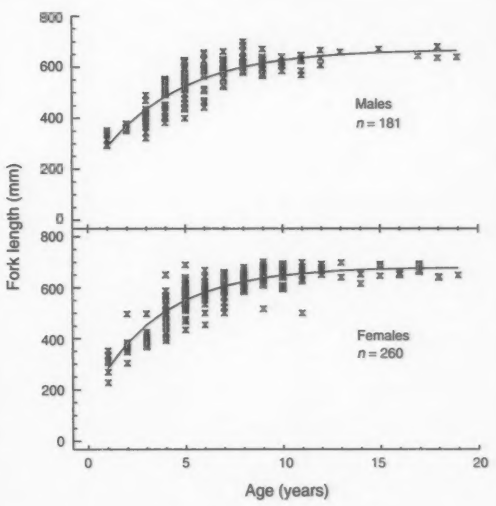

Figure 5

Observed and predicted lengths from the von Bertalanffy growth model for male and female bonefish, *Albula vulpes*.

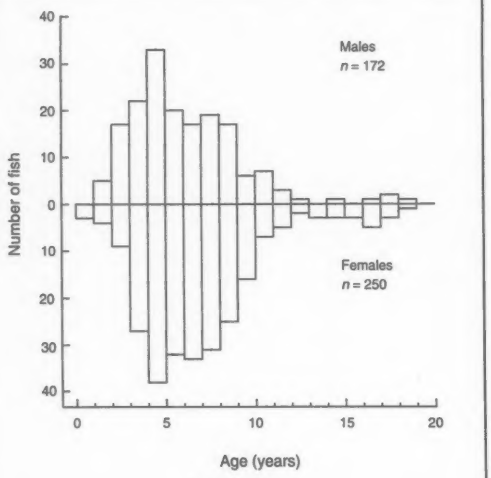

Figure 6

Age-frequency distributions for male and female Florida Keys bonefish, *Albula vulpes*, caught with hook-and-line gear.

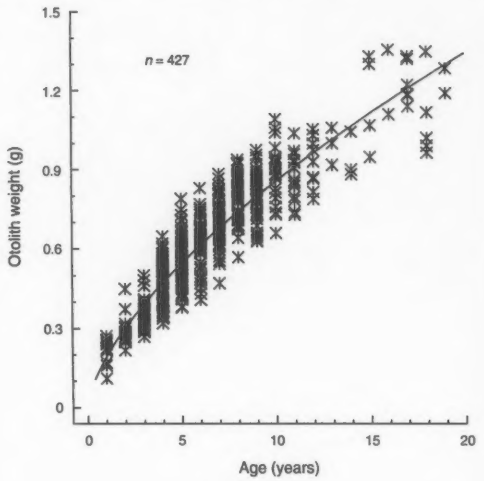

Figure 7

Growth of otoliths (g) of male and female bonefish, *Albula vulpes*. The equation for the regression of $\log_{10}$-transformed data is presented in Table 2.

females in our sample was slightly but significantly larger than that of males. This is also consistent with a small but significant difference in sex-specific growth rates; however, this finding is confounded by the significantly older median age of females, which would also contribute to the observed difference in the sex-specific size-frequency distributions. There is no readily apparent biological explanation for the slightly older age-frequency distribution of females in relation to males.

The only other estimates of von Bertalanffy growth parameters for bonefish are by Morales-Nin (1994) for 31 fish caught off Mexico's Pacific coast. She used a length-frequency analysis to estimate K=0.275 and L_∞ = 473 mm; her estimate of K is close to our Florida estimates, but her estimate of L_∞ is much less. Her small sample size could have seriously biased her parameter estimates. Furthermore, Pfeiler (1996) presented allozyme data that suggested that an undescribed species of *Albula* occurs off Mexico in the Gulf of California. It is unclear whether *A. vulpes* actually occurs off Mexico's Pacific coast or whether Morales-Nin's growth parameter estimates apply to *A. vulpes* or to Pfeiler's undescribed species.

The estimated instantaneous total mortality rate for bonefish was low. Our estimated range for natural mortality (0.2–0.3) included our total mortality estimates, suggesting that there is little fishing mortality. This was expected because the commercial harvest of bonefish from Florida waters is prohibited and most bonefish caught by recreational anglers are released. The low estimate for total mortality suggests that the mortality rate of bonefish caught with hook-and-line gear and then released was low, and that there was little mortality of bonefish as bycatch in commercial net fisheries operating in Florida Keys waters.

Otolith weight is not a precise estimator of bonefish age, but it could be used to approximate age distributions in situations where annulus counts are not available. Otolith weight accounted for more of the variability in age (84.9%) than fish length (77.0% for males and 79.2% for females). The Florida Keys are on the northern edge of the range of bonefish in the western North Atlantic. In specimens from the more tropical and less seasonal portions of the species' range, annuli may be more difficult to count and thus be less useful in age determination. This has been observed in other elopomorph species. Crabtree et al. (in press) reported that estimating age by sectioned otoliths was more difficult with tarpon from Costa Rican waters than it was with those from Florida waters; they rejected as unreadable more than twice as many otoliths from Costa Rican tarpon as those from Florida tarpon.

We cannot explain the presence of the two exceptionally small, old, and sexually mature female bonefish in our sample. Variable growth rates and stunting of some early maturing females is a possible ex-

planation. We cannot eliminate the possible existence of a cryptic species in the Keys, but the one specimen retained in our collection has no obvious morphometric or meristic characters to support this idea. Bruger (1974) also reported the occurrence of small bonefish from 221 to 352 mm FL with mature ovaries in the Florida Keys, but he found no morphometric or meristic evidence to suggest the presence of a second species. Additional specimens are needed to resolve this issue.

Acknowledgments

We thank Capt. John Kipp, who provided us with most of the bonefish examined in this study and without whose efforts this work would not have been possible. We also thank Capt. Mike Collins, the Florida Keys Fishing Guides Association, and the Islamorada bonefish tournaments for their support. Thanks to John Swanson, Bill Gibbs, and the staff at the Keys Marine Laboratory for their assistance; Jim Colvocoresses, John Hunt, and others at the South Florida Regional Laboratory for their cooperation; and Victor Neugebauer and Misty Cladas for their assistance. Jim Colvocoresses, Judy Leiby, Rich McBride, Mike Murphy, Jim Quinn, Tom Sminkey, and Dana Winkelman made helpful comments that improved the manuscript. This work was supported in part under funding from the Department of the Interior, U.S. Fish and Wildlife Service, Federal Aid for Sportfish Restoration, Project Number F-59.

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Marine stock-enhancement potential in nursery habitats of striped mullet, *Mugil cephalus*, in Hawaii

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Abstract.—Declines in world fishery landings have prompted new interest in the use of cultured fishes to help replenish depleted fish populations. The hypothesis that hatchery releases can increase population size has at least two corollaries that need to be tested: 1) released cultured fish survive, grow, and contribute to recruitment; and 2) cultured fish do not displace wild stocks. The former corollary is considered here for striped mullet, *Mugil cephalus* L., in nursery habitats.

Results from pilot experiments were used to modify release strategies to test marine stock enhancement potential in Kaneohe Bay, Hawaii. Of 80,507 native, cultured, striped mullet fingerlings tagged with coded wire and released during spring and summer, 2,642 fish were recovered by cast-net sampling during 11 months. Recapture rate increased 600% compared with initial studies in Kaneohe Bay. This increase was the result of confining releases to the vicinity of fresh-water streams and of imposing a minimum size of 70 mm TL during summer releases. After 11 months, cultured fish represented 50% of the striped mullet in collections at the release site, 20% in a nursery habitat 1 km to the north, and 10% in a nursery 3 km north. The location of releases (stream mouth vs. upstream lagoon) significantly affected dispersal patterns but did not affect growth or recapture rate. This study corroborated earlier results which showed that the smallest fish released (45–60 mm) could survive relatively well if released in spring. At least three measures were needed to describe hatchery effect: 1) hatchery contribution (% cultured fish in samples), 2) catch per unit of effort for cultured and wild striped mullet, and 3) recovery rate (no. captured/no. released). This study documents that survival of cultured fish in coastal nurseries can be significantly improved by using information from pilot release experiments to revise release parameters.

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The need for improved understanding and management of coastal fisheries is clear (New, 1991; NMFS, 1991, 1992; Anthony, 1993; Sissenwine and Rosenberg, 1993; Schnute and Richards, 1994). In 1990, growth in annual world fishery production peaked at 100 million metric tons (t) (FAO, 1992). Without more effective control of marine fisheries, seafood availability and recreational fishing opportunities are likely to decline at a rapid pace as demand increasingly outweighs supply during the next century (New, 1991; FAO, 1992). Ricker (1969) estimated maximum sustainable annual production levels of wild fisheries may be limited to 160 million t. More recently, the Food and Agriculture Organization of the United Nations (FAO) revised the estimate to 100 million t (WRI, 1990). Larkin (1993) suggests that sea farming could increase annual yields several fold over this level.

One form of sea farming, supplementing wild stocks with releases of cultured organisms (hatchery-based stock enhancement), may have considerable potential in marine and estuarine environments. Whether stock enhancement can help significantly increase world production levels of seafood is unclear (Schnute and Richards, 1994; Smedstad et al., 1994). Increased emphasis on quantitative evaluation is needed to determine the actual potential of stock enhancement. Norway and the United States first conducted large-scale hatchery releases of yolk-sac larvae of marine fishes at the end of the last century (Solemdal et al., 1984; Grimes, 1995); Japan followed with releases of hatched larvae of cod, herring, and king crab in the early 1900's (called "sea farming" in Japan; Kitada et al., 1992; Honma, 1993). A century later, the central issue remains largely unresolved—can propagation and release of cultured marine organisms into the wild increase coastal fish populations?

Although marine stocking programs in the USA were abandoned earlier this century for lack of a clear impact on fisheries landings, the potential for using hatchery releases to increase populations of coastal fishes was never critically tested (Richards and Edwards, 1986). Now, modern marking methods and new aquaculture capabili-

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ties provide the technologies required to quantify and evaluate marine stock enhancement (Jefferts et al., 1963; Buckley and Blankenship, 1990; and see Honma, 1993, for examples of growth in marine aquaculture). There is an emerging optimism that carefully implemented marine stock enhancement might be a useful fisheries management tool (e.g. Grimes, 1995). Use of cultured marine organisms to help replenish depleted coastal stocks has finally begun to receive empirical evaluation (Tsukamoto et al. 1989; Svåsand and Kristiansen, 1990; Svåsand et al., 1990, 1991; Bannister and Howard, 1991; Barlow and Gregg, 1991; Kitada et al., 1992, 1994; Iglesias and Rodríguez-Ojea, 1994; Jørstad et al., 1994, a and b; Nordeide et al., 1994; Smedstad et al., 1994; Stoner, 1994; Støttrup et al., 1994; Kent et al., 1995; Leber, 1995; Leber et al., 1995; Willis et al., 1995).

The hypothesis that hatchery releases can help increase marine fish populations has at least two corollaries that need to be tested. One is that cultured fishes released into coastal waters actually survive, grow, and contribute to recruitment. The other corollary is that cultured fish do indeed increase abundance rather than displace wild stocks. These two postulates are basic assumptions of stock-enhancement theory, yet both remain largely untested in coastal ecosystems (i.e. with organisms that reproduce in marine environments). The former corollary is the focus of this study, the latter is considered elsewhere (Leber et al., 1995).

A series of workshops was held to select species for immediate stock-enhancement research in Hawaii. The species given priority was Pacific threadfin, *Polydactylus sexfilis*, an inshore carnivore. An inshore herbivore, striped mullet, *Mugil cephalus*, ranked second in this semi-quantitative selection process (Leber[1]). We chose to begin field experiments with striped mullet because it ranked high in the selection process and culture techniques were available. We expected to apply lessons learned about stock enhancement to Pacific threadfin once culture techniques became available.

To design a rigorous test, data would be needed from pilot releases to define effective release strategies. Fish size-at-release (SAR) and the timing of releases were important choices that needed to be made, as Hager and Noble (1976) and Bilton et al. (1982) had already shown with coho salmon released into streams in the Pacific northwest. Releasing fish into coastal environments would also require careful consideration of release habitat. If any of these three variables affected survival of released fish, they would also affect the power of any test of stock-enhancement potential. In Hawaii, a series of pilot release experiments were conducted to identify effects of release magnitude, SAR, release habitat, and release season on survival and contribution of cultured striped mullet to wild stock abundance (Leber, 1995; Oceanic Institute[2]; Leber et al.[3]). The results of those pilot releases were used to design the present study, which is to test the first corollary—that cultured fish make a substantial contribution to a marine fish population in Hawaii.

As pilot release-recapture experiments began in Hawaii, Tsukamoto et al. (1989) published results that indicated that SAR affected survival of red sea bream, *Pagrus major*, juveniles released into News Bay, Japan. In 1990, Svåsand and Kristiansen (1990) showed similar results with cod, *Gadus morhua*, released into Norwegian fjords. In 1990, a similar pattern was observed in Hawaii following summer releases of about 40,000 tagged striped mullet into each of two embayments on Oahu, Maunalua Bay and Kaneohe Bay (Leber, 1995). Work with striped mullet revealed that recapture rates approached zero when cultured fish smaller than 60-mm total length (TL) were released in summer or fall months. These results ruled out the alternative of stocking newly hatched fry or postlarvae in an experimental test of the stock-enhancement concept in Hawaii. Pilot releases in Hawaii also revealed that survival of cultured mullet was strongly affected by release habitat and release season (Leber, 1995; Leber and Arce, in press; Leber et al.[3]). Hatchery release studies with marine fishes in Norway, Florida, and California (Svåsand and Kristiansen, 1990; Drawbridge et al., 1995; Willis et al., 1995) and with cultured conch released in the Caribbean (Stoner, 1994) have shown substantial effects of release strategies on survival in coastal environments.

Based on the results of pilot hatchery releases in Kaneohe Bay, an experiment was designed to incorporate improved release strategies and to evaluate the potential of using hatchery releases to increase significantly juvenile striped mullet recruitment in Kaneohe Bay, the largest estuary in Hawaii. Criteria for success were the following: 1) cultured fish released in this study represented a substantial pro-

[1] Leber, K. M. 1994. Prioritizing marine fishes for stock enhancement in Hawaii. The Oceanic Institute, Honolulu, HI, 46 p.

[2] Oceanic Institute. 1990. Stock enhancement of marine fish in the State of Hawaii (SEMFISH, Phase II). Annual report to NMFS, February 1989–June 1990, Waimanalo, Hawaii, 106 p.

[3] Leber, K. M., S. M. Arce, H. L. Blankenship, and N. P. Brennan. 1996. Influence of release season on size-dependent survival of cultured striped mullet, *Mugil cephalus*, in a Hawaiian estuary. In review.

portion (at least 20%) of the juvenile striped mullet in net samples 4 months after release; 2) there was a persistence of cultured fish in net samples throughout the study; and 3) growth was comparable to measured rates in wild juveniles. If these criteria were met, it would be reasonable to assume that cultured fish had substantially affected juvenile recruitment at the study site.

This study was conducted in and around fresh water tributaries, the preferred nursery habitat for striped mullet. Striped mullet are catadromous and begin to move out of their nursery habitats as they approach maturity (Blaber, 1987). In Hawaii, yearling juveniles begin to move out of the intertidal zone and out of shallow shore zones of streams by about February or March (Major, 1978; Leber, 1995; Oceanic Institute[4]). Striped mullet reach advanced sexual development in fresh water but must migrate to the sea to spawn (Blaber, 1987). Annual recruitment into inshore nursery habitats of young-of-the-year wild mullet occurs in spring in Hawaii (Major, 1978).

Methods

Hatchery releases

Striped mullet were spawned from wild broodstock at The Oceanic Institute and reared to fingerling size for spring and summer releases. Batches of striped mullet eggs were hatched about every six weeks over a five-month period. Larval striped mullet from each batch were hatched and cultured in 5,000-L cylindrical tanks with conical bottoms for 45 days. Stage-1 juveniles (45 days old, 20 mm TL) were transferred to 8,000-L circular tanks and nursed for 40 days to stage-2 juveniles (85 days old, 40 mm TL). Stage-2 juveniles were transferred to 30,000-L circular tanks and nursed to tagging size (45–130 mm TL). In culture tanks, growth rates averaged 0.5 mm TL/day.

A release-recapture experiment was performed to evaluate recapture rates of cultured striped mullet. Release magnitude, release location, release season, and size of fish released were determined from results of 1990 and 1991 pilot studies in Kaneohe Bay (Leber, 1995; Leber et al.[3]). During 4 May through 29 May 1992, and again from 13 July through 7 August 1992, juveniles were harvested from culture tanks, graded into five different length groups (ranging from 45 mm to 130 mm TL) by using commercial bar graders and tagged with binary coded-wire tags (CWT) (Northwest Marine Technology, Inc., Olympia, WA). Prior to tagging, fish were provided a 2-day period to recover from stress of harvesting and size grading. About 80,500 tagged fish were released into Kaneohe Bay.

Tags identified year and season of release, SAR, release habitat, release lot (date), and number of fish released per treatment condition. Fish were tagged in batches, with a different code for each season-SAR-site-lot combination. Tags were implanted in the snout area with an automatic injector with head molds designed specifically for striped mullet.

For each release season and SAR combination, the experiment was replicated with three release lots at each of two release locations in Kahaluu Stream (Fig. 1), where the greatest recruitment of wild mullet in Kaneohe Bay had been reported (Leber, 1995; Oceanic Institute[4]). In May, fish of all five size intervals were released in each lot (45–60 mm; 60–70 mm; 70–85 mm; 85–110 mm; and 110–130 mm). Only fish of

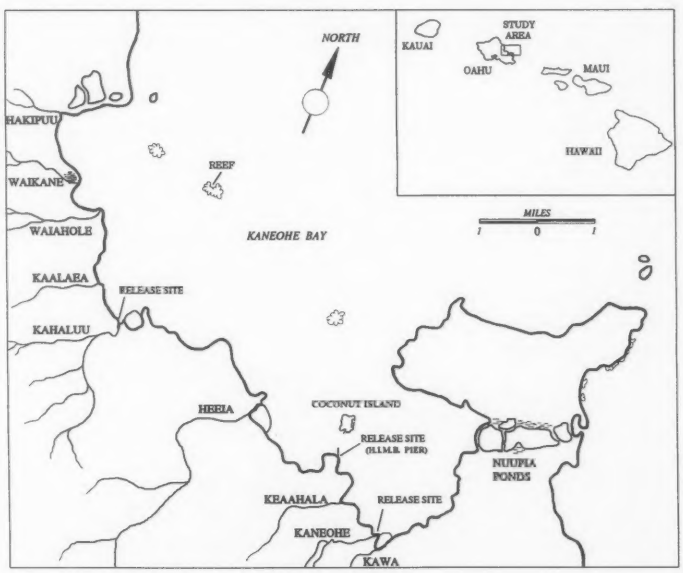

Figure 1

Map of Kaneohe Bay showing pilot study release sites and nursery habitats where monthly cast-net collections were conducted. In this study, all releases were made at Kahaluu Stream, a principal nursery habitat for striped mullet in Kaneohe Bay.

[4] Oceanic Institute. 1991. Stock enhancement of marine fish in the State of Hawaii (SEMFISH Phase III). Annual report to NMFS, June 1990–June 1991. Waimanalo, Hawaii, 107 p.

the three largest size intervals were released in summer (none <70 mm TL). There was size variation in all batches of mullet reared for this study. However, the primary difference among the five size intervals of fish released was fish age.

Replicate release lots were introduced biweekly for a 3- to 4-week period in both spring and summer. Fish were transported and then released simultaneously at the stream inlet and 300 m upstream in a 10-ha lagoon. Numbers of tagged and released fish varied between seasons and among size intervals released but were held nearly constant among release lots and between release sites (Table 1). Between 10,200 and 15,100 tagged fish were released in each of six release lots. Releases were conducted around mid-day or early afternoon. Bottom salinities at release sites ranged from 12 to 25 ppt. All releases were made near the shoreline in water from 0.5 to 1.5 m deep.

Previous studies revealed a CWT retention rate of 97% for striped mullet during 12 months following tagging (Oceanic Institute[4]). To verify tag-retention rates in this study, at least 5% of fish tagged for each release lot were randomly subsampled prior to each release. These subsamples, totalling 4,264 tagged fish, were retained in 12 tanks for up to 4 months; fish were checked monthly to verify when % tag retention stabilized (Blankenship, 1990).

Tagged fish from the 1991 study were also recovered in this study. Methods in that study were essentially identical to those here, with two exceptions: 1) in 1991, fish of all five size intervals were released in both spring and summer; 2) 1991 release sites included Kahaluu Stream mouth and Kaneohe Stream mouth (Leber et al.[3]). The mouth of Kaneohe Stream lies 11.6 km south of Kahaluu Stream mouth.

Monitoring

To evaluate the effect of releases on juvenile abundance, collections were made monthly with cast nets in four Kaneohe Bay nursery habitats, except for July (when summer releases were conducted). We began to monitor abundances of released and wild striped mullet in Kaneohe Bay on 8 June 1992 and continued to do so for 10 months. Each field collection was conducted during a 1-wk period. Collections were made during the day during an 8-h period at each nursery site (sampling station). Stations were established in the vicinity of documented striped mullet nursery habitats at various tributaries throughout the bay (Oceanic Institute[4]).

To standardize collection effort, two substations were established at each station—one 200 to 300 m upstream, the other in the bay seaward of the stream mouth and on subtidal reef flats running along the bay shore on both sides of the stream mouth. Within substations, 15 cast-net throws were made. A total of 120 cast-net samples were taken each month. To broaden the range of microhabitats and fish size-

Table 1

Summary statistics for 80,507 fish tagged and released in 1992 to evaluate hatchery releases in Kaneohe Bay. Unique batch codes were used to identify fish from each cell in the matrix. Spring release lot 1 occurred on 4 May, lot 2 on 15 May, and lot 3 on 29 May. Summer release lot 1 occurred on 13 July, lot 2 on 24 July, and lot 3 on 7 August.

Release site	Size at release	Release season								Grand total
		Spring release lot				Summer release lot				
		1	2	3	Total	1	2	3	Total	
Kahaluu (upstream at lagoon)	45–60 mm	2,356	2,368	2,277	7,001	0	0	0	0	7,001
	60–70 mm	2,372	2,375	2,371	7,118	0	0	0	0	7,118
	70–85 mm	1,595	1,594	1,591	4,780	2,867	2,497	4,063	9,427	14,207
	85–110 mm	807	807	805	2,419	2,863	2,493	2,540	7,896	10,315
	110–130 mm	398	399	399	1,196	250	125	72	447	1,643
	Subtotal	7,528	7,543	7,443	22,514	5,980	5,115	6,675	17,770	40,284
Kahaluu Stream (mouth)	45–60 mm	2,356	2,369	2,321	7,046	0	0	0	0	7,046
	60–70 mm	2,361	2,370	2,344	7,075	0	0	0	0	7,075
	70–85 mm	1,596	1,593	1,599	4,788	2,878	2,494	4,069	9,441	14,229
	85–110 mm	806	806	805	2,417	2,848	2,500	2,540	7,888	10,305
	110–130 mm	396	399	399	1,194	249	125	0	374	1,568
	Subtotal	7,515	7,537	7,468	22,520	5,975	5,119	6,609	17,703	40,223
Grand total		15,043	15,080	14,911	45,034	11,955	10,234	13,284	35,473	80,507

ranges sampled, two different-size cast nets were used. Of the 15 casts per substation, 10 were made with a 5-m diameter, 10-mm mesh net, and five casts were made with a 3-m diameter, 6-mm mesh net. The smaller net was more effective in narrow upstream habitats.

We used stratified-random sampling; cast nets were thrown over schools of mullet juveniles, rather than thrown randomly. Random sampling yielded few wild mullet and very few tagged individuals. Cultured and wild striped mullet schooled together in fairly low densities within these clear-water nursery habitats, and our collections targeted these schools. Nevertheless, data used to determine recapture rates and proportions of tagged mullet in samples were randomly distributed because there was no a-priori indication that schools, once sighted, contained tagged individuals.

Mullet sampled in these collections were measured and checked for tags with a portable tag detector (Northwest Marine Technology, Inc.). All tagged mullet were placed on ice and returned to the laboratory for size measurement and tag analysis. Wild fish were counted, measured, and released at the sample site. After extraction, the binary codes were read by a technician with a binocular microscope (40×). All tag codes were verified with a second (blind) reading by a another technician.

Data were analyzed with SYSTAT software (Wilkinson, 1990). A randomized-block design ANOVA was used to compare means. Treatments (SAR, release microhabitat) were blocked over time (3 release lots) within season (spring and summer). Proportions were arcsine transformed. Orthogonal contrasts were used to compare means (Sokal and Rohlf, 1981). SYSTAT Basic was used to write tag decoding algorithms. For each recaptured fish, the algorithms identified SAR, release microhabitat, release date, release lot, and number of fish released per treatment-lot combination on the basis of the binary tag codes. An error-check algorithm was also written. Variance estimates are expressed throughout as standard errors.

Results

Recapture summary

A total of 2,985 tagged cultured mullet were recaptured during the 11-month period of this study (Table 2). Of these, 2,642 were cultured fish from the present study (1992 releases). None of the fish released in 1992 were recaptured at Kaneohe Stream. From the tag codes it was determined that 304 (10.2%) of the 2,985 tagged fish collected had been released in

Table 2

Numbers of tagged cultured striped mullet recovered in cast-net samples made in Kaneohe Bay. 304 of the 2,985 cultured fish recaptured were released in 1991, the remainder in 1992. None of the fish released in 1992 were captured at Kaneohe Stream. Sites are arranged from north (Waiahole Stream) to south (Kaneohe Stream). 30 cast-net throws were made at each station monthly.

Collection site	Source	Jun	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	Total	Mean	SE
Waiahole Stream	Wild	126	169	141	121	10	65	54	13	47	26	772	77.2	18.2
	Cultured	29	26	27	64	15	47	32	8	7	3	258	25.8	6.0
	%Cultured	18.7	13.3	16.1	34.6	60.0	42.0	37.2	38.1	13.0	10.3	25.0	28.3	5.2
Kaalaea Stream	Wild	84	154	66	172	85	58	48	34	24	20	745	74.5	16.4
	Cultured	111	221	83	58	128	74	60	46	22	5	808	80.8	19.5
	%Cultured	56.9	58.9	55.7	25.2	60.0	56.1	55.6	57.5	47.8	20.0	52.0	49.4	4.6
Kahaluu Stream	Wild	258	99	82	69	65	49	34	64	32	28	780	78.0	24.7
(1991 and 1992	Cultured	231	376	237	188	164	111	136	132	37	28	1640	164.0	32.4
release site in	% Cultured	47.2	79.2	73.7	73.2	71.6	69.4	80.0	67.4	53.6	50.0	67.8	66.5	3.8
N. Kaneohe Bay)														
Kaneohe Stream	Wild	58	36	55	56	50	45	35	27	48	40	450	45.0	3.3
(1991 release site	Cultured	41	29	42	42	33	21	33	11	19	8	279	27.9	4.0
in S. Kaneohe Bay)	%Cultured	41.4	44.6	43.3	42.9	39.8	31.8	48.5	29.0	28.4	16.7	38.3	36.6	3.1
All streams	Wild	526	458	344	418	210	217	171	138	151	114	2747	274.7	47.2
	Cultured	412	652	389	352	340	253	261	197	85	44	2985	298.5	55.2
	%Cultured	43.9	58.7	53.1	45.7	61.8	53.8	60.4	58.8	36.0	27.8	52.1	50.0	3.5

Kaneohe Bay in 1991 as part of a previous pilot study (Leber et al.[3]). Tags from 39 (1.3%) of the recaptured fish were lost during the extraction process. These 39 cultured fish were released either in 1991 or 1992 but could not be further identified and were excluded from our analyses. Thus, the decoded tag data are based on 2,946 tags.

Tag retention in the subsampled fish held for 4 months averaged 97.9% (±0.6 SE, n=12 tanks). With one exception (92.6%, lot 1, lagoon release), all tag retention rates within release lots exceeded 97%. After capture data were adjusted for the 2.1% tag loss, a total of about 2,697 cultured fish from the 1992 releases were actually captured (3.3% of the 80,507 fish released in this study).

Tagged cultured fish represented about 50% of the 5,732 wild and cultured mullet collected from the four study sites (Table 2). Proportions of cultured mullet in Kahaluu samples remained >50% of the total (wild and cultured) mullet sampled in collections throughout the study and were ≥70% in six of ten collections (Table 2). Proportions of hatchery fish were also high at two streams north of the release site.

Recovery of yearlings released in 1991

Sampling periods in the present study ranged from 47 weeks to 100 weeks after the 1991 releases. Most (86%) fish from 1991 releases were collected at Kaneohe Stream, where they represented a high proportion of 1-yr-old mullet at that site throughout their second year in the wild (Table 3). Only 42 of the 304 fish from the 1991 release were collected outside Kaneohe Stream. These 42 fish accounted for <3% of the cultured fish collected at any other site. Thus, some fish from 1991 releases continued to occupy juvenile mullet nursery habitats well into their second year.

Marine enhancement impact: 1992 releases

Release impact in nursery habitats About 90% of the 2,946 tags recovered and decoded were from striped mullet released at Kahaluu in 1992. These fish made a substantial contribution to juvenile recruitment in three nursery habitats in the north end of the bay: Kahaluu Stream, Kaalaea Stream, and Waiahole Stream (Table 2).

Impact of the test release was greatest at the release site, Kahaluu Stream; there was a trend towards reduced impact with shoreline distance away from that site. Cultured fish consistently outnumbered wild fish at the release site and averaged 66% of the mullet in monthly collections at Kahaluu. After 11 months in the wild, cultured fish still represented 50% of the mullet sampled at Kahaluu. Greatest impact outside of the release site was seen at Kaalaea, 1 km north of Kahaluu Stream, where cultured fish averaged about 50% of the mullet sampled. A substantial effect was also apparent in Waiahole Stream, a mullet nursery habitat 3 km north of Kahaluu Stream, where cultured fish averaged 28% of the mullet sampled. Proportions of cultured mullet in collections were stable through time at all four nursery habitats sampled until spring, when annual recruitment of wild mullet began. Numbers of both wild and cultured fish from the 1992 year class declined in samples in spring at all nursery sites (Table 2).

Table 3

Movement patterns following 1991 releases of 91,245 tagged cultured mullet in Kaneohe Bay (half at Kahaluu Stream, half at Kaneohe Stream.) Release season and release site are identified for 304 tagged fish recovered at the various collection (recapture) sites throughout the Bay. Recapture sites (and distances travelled) are ordered geographically within collection dates, from the northernmost site (Waiahole Stream) to the southernmost site (Kaneohe Stream) at which tagged fish were collected (see Fig. 1). Data are totals (n) recaptured in 300 cast-net samples per site taken over the 10-mo. study period.

Collection date (weeks after release)	Recapture site	Kahaluu release n	Kahaluu release Distance (km)	Kaneohe release n	Kaneohe release Distance (km)
Spring release					
Weeks 57–100	Waiahole	—	3.05	3	15.00
	Kaalaea	3	0.98	—	12.59
	Kahaluu	26	0	—	12.04
	Kaneohe	—	11.58	111	0
	Total	29		114	
Summer release					
Weeks 47–91	Waiahole	1	3.05	3	15.00
	Kaalaea	—	0.98	—	12.59
	Kahaluu	6	0	—	12.04
	Kaneohe	1	11.58	150	0
	Total	8		153	

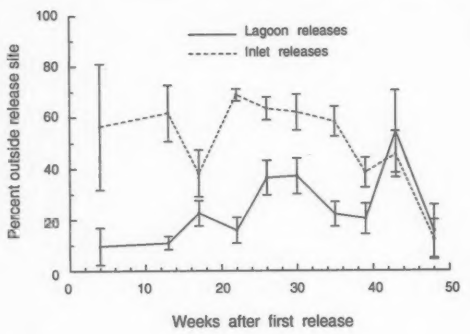

Figure 2

Release microhabitat effect on dispersal of released cultured fish. Proportions (± SEM, n=6 lots) of cultured striped mullet recaptured outside of the release habitat, Kahaluu Stream, following downstream (inlet) releases at the shore next to the stream mouth, and releases 300 m upstream (lagoon).

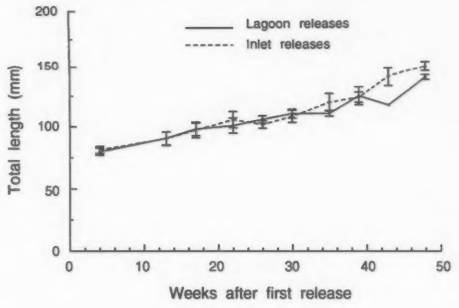

Figure 3

Mean length (TL [±SEM, n=6]) of cultured striped mullet recovered in net samples made over the course of the study, for individuals that were 70–85 mm TL when released.

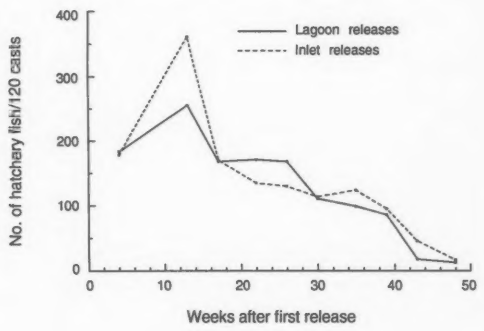

Figure 4

Catch per unit of effort (CPUE) for cultured striped mullet from collections made at four nursery habitats (combined data) in Kaneohe Bay, including the release site. Total number of tagged fish recaptured in 120 cast-net samples taken monthly (30 samples per month at each nursery habitat) compared with those taken over the 11-mo study period.

Release microhabitat effect on enhancement impact Initial habitat selection was strongly affected by release microhabitat. There was greater dispersal away from the release site by fish released next to the inlet of Kahaluu Stream than by fish released about 300 m upstream in the lagoon (Fig. 2.) This pattern was similar following both spring and summer releases (Table 4). Most fish released upstream remained in Kahaluu Stream throughout the study, whereas most fish from the inlet releases moved to other nursery sites in the bay. This difference in dispersal patterns was statistically significant by the second collection date (P<0.003, n=6 release lots per treatment [3 spring + 3 summer]) and was observed through mid February 1993 (P<0.01 in collections Aug, Oct, and Jan; P<0.05 in Nov, Dec, and Feb; not significant in Jun, Sep, Mar, and Apr).

Recapture rates and growth rates were unaffected by release microhabitat. Growth curves for fish released at the inlet and lagoon were intermingled (Fig. 3) as were plots of numerical abundances of cultured fish in collections (Fig. 4). Statistical comparisons were nonsignificant (n=6, P>0.08) for all collection dates.

SAR and release-season effects on enhancement impact

Overall SAR effect on recapture rates Fish size-at-release affected survival of mullet released in this study. The smallest size group (45–60 mm TL) had significantly reduced survival in comparison with other sizes (Fig. 5). Fish <60 mm TL were recaptured at less than half the frequency of larger fish released (Fig. 5; P<0.001; P<0.002 in orthogonal contrast in a comparison of SAR-1 with SAR1-2, -3, and -4 combined; n=6 with recapture data from spring and summer releases combined). For the four SAR groups >60 mm TL (in the aggregate data set, spring and summer releases combined), there were no significant differences among recapture frequencies (P>0.30 for any comparison, spring and summer releases combined).

Table 4

Movement patterns following 1992 releases at Kahaluu Stream in Kaneohe Bay. Release season and release sites (inlet release was at the mouth of Kahaluu Stream and lagoon release was about 300 meters upstream in a 10-hectare lagoon) are identified for tagged fish recovered at the various collection (recapture) sites throughout the Bay. Recapture sites (and distances travelled) are ordered geographically within collection dates, from the northernmost site (Waiahole Stream) to the southernmost site (Kaneohe Stream) at which tagged fish were collected (see Fig. 1). Monthly data are totals (n) per 30 samples per site, organized by the average time (weeks after release) that fish had been in the wild prior to collection.

Collection date (weeks after release)	Recapture site	Inlet release n	Inlet release Distance (km)	Lagoon release n	Lagoon release Distance (km)
Spring release					
8–12 Jun 92	Waiahole	25	3.1	4	3.2
	Kaalaea	100	1.0	10	1.1
	Kahaluu	53	0	169	.1
3	Kaneohe	—	11.6	—	11.7
	Total	178		183	
17–21 Aug 92	Waiahole	18	3.1	—	3.2
	Kaalaea	131	1.0	10	1.1
	Kahaluu	25	0	67	.1
13	Kaneohe	—	11.6	—	11.7
	Total	174		77	
21–25 Sep 92	Waiahole	11	3.1	4	3.2
	Kaalaea	38	1.0	13	1.1
	Kahaluu	34	0	54	.1
18	Kaneohe	—	11.6	—	11.7
	Total	83		71	
19–23 Oct 92	Waiahole	14	3.1	3	3.2
	Kaalaea	28	1.0	5	1.1
	Kahaluu	20	0	81	.1
22	Kaneohe	—	11.6	—	11.7
	Total	62		89	
16–23 Nov 92	Waiahole	3	3.1	2	3.2
	Kaalaea	25	1.0	17	1.1
	Kahaluu	17	0	46	.1
26	Kaneohe	—	11.6	—	11.7
	Total	45		65	
14–18 Dec 92	Waiahole	5	3.1	5	3.2
	Kaalaea	17	1.0	8	1.1
	Kahaluu	19	0	37	.1
30	Kaneohe	—	11.6	—	11.7
	Total	41		50	
11–15 Jan 93	Waiahole	8	3.1	4	3.2
	Kaalaea	21	1.0	2	1.1
	Kahaluu	17	0	27	.1
34	Kaneohe	—	11.6	—	11.7
	Total	46		33	
Summer release					
17–21 Aug 92	Waiahole	6	3.1	1	3.2
	Kaalaea	67	1.0	12	1.1
	Kahaluu	114	0	165	.1
3	Kaneohe	—	11.6	—	11.7
	Total	187		178	
21–25 Sep 92	Waiahole	10	3.1	2	3.2
	Kaalaea	12	1.0	15	1.1
	Kahaluu	65	0	80	.1
8	Kaneohe	—	11.6	—	11.7
	Total	87		97	
19–23 Oct 92	Waiahole	32	3.1	14	3.2
	Kaalaea	20	1.0	5	1.1
	Kahaluu	21	0	63	.1
13	Kaneohe	—	11.6	—	11.7
	Total	73		82	
16–23 Nov 92	Waiahole	3	3.1	6	3.2
	Kaalaea	49	1.0	35	1.1
	Kahaluu	33	0	62	.1
16	Kaneohe	—	11.6	—	11.7
	Total	85		103	
14–18 Dec 92	Waiahole	18	3.1	18	3.2
	Kaalaea	35	1.0	13	1.1
	Kahaluu	20	0	30	.1
20	Kaneohe	—	11.6	—	11.7
	Total	73		61	
11–15 Jan 93	Waiahole	14	3.1	5	3.2
	Kaalaea	27	1.0	10	1.1
	Kahaluu	37	.1	51	.1
24	Kaneohe	—	11.6	—	11.7
	Total	78		66	
15–19 Feb 93	Waiahole	3	3.1	4	3.2
	Kaalaea	23	1.0	6	1.1
	Kahaluu	33	0	23	.1
29	Kaneohe	—	11.6	—	11.7
	Total	59		33	
15–19 Mar 93	Waiahole	2	3.1	4	3.2
	Kaalaea	11	1.0	2	1.1
	Kahaluu	16	0	4	.1
34	Kaneohe	—	11.6	—	11.7
	Total	29		10	

Table 4 (continued)

Collection date (weeks after release)	Recapture site	Inlet release n	Inlet release Distance (km)	Lagoon release n	Lagoon release Distance (km)
Spring release					
16–19 Dec 93	Waiahole	—	3.1	1	3.2
	Kaalaea	13	1.0	4	1.1
	Kahaluu	23	0	48	.1
39	Kaneohe	—	11.6	—	11.7
	Total	36		53	
15–19 Mar 93	Waiahole	—	3.1	1	3.2
	Kaalaea	8	1.0	1	1.1
	Kahaluu	9	0	6	.1
43	Kaneohe	—	11.6	—	11.7
	Total	17		8	
12–16 Apr 93	Waiahole	—	3.1	—	3.2
	Kaalaea	3	1.0	—	1.1
	Kahaluu	6	0	4	.1
47	Kaneohe	—	11.6	—	11.7
	Total	9		4	
Grand totals through Week 39	Waiahole	84	3.1	23	3.2
	Kaalaea	373	1.0	69	1.1
	Kahaluu	208	0	529	.1
	Kaneohe	—	11.6	—	11.7
	Total	665		621	
Summer release					
12–16 Apr 93	Waiahole	—	3.1	2	3.2
	Kaalaea	—	1.0	2	1.1
	Kahaluu	8	0	5	.1
38	Kaneohe	—	11.6	—	11.7
	Total	8		9	
Grand totals through Week 38	Waiahole	88	3.1	56	3.2
	Kaalaea	244	1.0	100	1.1
	Kahaluu	347	0	483	.1
	Kaneohe	—	11.6	—	11.7
	Total	679		639	

Effect of release season Although recapture rates among SAR groups >60 mm appeared similar in the aggregate data set, an SAR effect was apparent when data were collapsed within release seasons (Table 5). To clarify survival and the interactive effect of release season with SAR, only fish that survived at least 16 weeks are included in Figures 6, 7, and 8. This provides a picture of those cultured fish that remain in the population from 4 months on, having survived initial causes of mortality in the wild, and that have the potential to affect adult abundances.

All sizes released in spring and summer were prominent in cast-net collections (Table 5). As expected following spring releases (Leber et al.[3]), no direct relationship was apparent between SAR and recapture rates. However, recapture rates (from week 16 on) were significantly less for the smallest size group released than for SAR groups 2, 3, and 5 (Fig. 6, $P<0.02$).

Summer releases resulted in better recovery of the largest size group released (Fig. 7, 110–130 mm TL; $P<0.04$; marginally significant). There was also a trend (nonsignificant) towards better recovery of the three largest SAR groups when released in summer rather than in spring (Fig. 8).

Growth of fish released in spring was comparable with that of fish released in summer (Fig. 9). Data in Figure 9 are for fish from the median SAR group (70–85 mm TL), for which the greatest amount of data was available. This growth comparison is representative of the other sizes released in both seasons.

Comparison with 1990 and 1991 release impact There was substantially greater impact on juvenile abundances in Kaneohe Bay following 1992 releases than after pilot releases in 1990 (Leber, 1995) and in 1991 (Leber et al.[3]). Proportions of cultured fish at Kahaluu 10 months after releases increased from about 3% following 1990 releases to 10% after 1991 releases, to about 50% in the present study (Fig. 10).

The general pattern following releases was similar in all years—an initial increase in proportions of cultured fish in samples, followed by a decline over the next year. However, there were two principal differences in 1992: 1) July releases in 1992 caused a considerably greater increase in abundance than in

Table 5

Numbers of tagged fish released in 1992 and recovered from each treatment group by size at release within release season at Kahaluu Stream in Kaneohe Bay. Data are totals (n) recaptured and recapture frequencies (% recap. [n recaptured/n released]), organized by the average time (weeks after release) that fish had been in the wild prior to collection. Note that summer releases followed spring releases by 10 weeks.

Collection date (weeks after release)	Size at release	Total recap. n	% recapt.	Collection date (weeks after release)	Size at release	Total recap. n	% recapt.	Grand total	Grand total % recap.
Spring release				**Summer release**					
8–12 Jun 92	45–60 mm	14	0.10	17–21 Aug 92	45–60 mm	—	—	14	0.10
	60–70 mm	98	0.69		60–70 mm	—	—	98	0.69
	70–85 mm	131	1.37		70–85 mm	161	0.85	292	1.03
3	85–110– mm	89	1.84	3	85–110 mm	192	1.22	281	1.36
	110–130 mm	29	1.21		110–130 mm	12	1.46	41	1.28
	Total	361	0.80		Total	365	1.03	726	0.90
				21–25 Sep 92	45–60 mm	—	—	—	—
					70–85 mm	—	—	—	—
					70–85 mm	76	0.40	76	0.40
				8	85–110 mm	106	0.68	106	0.68
					110–130 mm	2	0.24	2	0.24
					Total	184	0.52	184	0.52
17–21 Aug 92	45–60 mm	30	0.21	19–23 Oct 92	45–60 mm	—	—	30	0.21
	60–70 mm	98	0.69		60–70 mm	—	—	98	0.69
	70–85 mm	77	0.80		70–85 mm	82	0.43	159	0.56
13	85–110 mm	37	0.77	13	85–110 mm	70	0.51	107	0.52
	110–130 mm	9	0.38		110–130 mm	3	0.37	12	0.37
	Total	251	0.56		Total	155	0.44	406	0.50
21–25 Sep 92	45–60 mm	20	0.14	16–23 Nov 92	45–60 mm	—	—	20	0.14
	60–70 mm	55	0.39		60–70 mm	—	—	55	0.39
	70–85 mm	49	0.51		70–85 mm	104	0.55	153	0.54
18	85–110 mm	18	0.37	16	85–110 mm	78	0.49	96	0.47
	110–130 mm	12	0.50		110–130 mm	6	0.73	18	0.56
	Total	154	0.34		Total	85	0.53	342	0.42
19–23 Oct 92	45–60 mm	44	0.31	14–18 Dec 92	45–60 mm	—	—	44	0.31
	60–70 mm	68	0.48		60–70 mm	—	—	68	0.48
	70–85 mm	25	0.26		70–85 mm	60	0.32	85	0.30
22	85–110 mm	6	0.12	20	85–110 mm	68	0.43	74	0.36
	110–130 mm	8	0.33		110–130 mm	6	0.73	14	0.44
	Total	151	0.34		Total	134	0.38	285	0.35
16–23 Nov 92	45–60 mm	29	0.21	11–15 Jan 93	45–60 mm	—	—	29	0.21
	60–70 mm	36	0.25		60–70 mm	—	—	36	0.25
	70–85 mm	28	0.29		70–85 mm	84	0.45	112	0.39
26	85–110 mm	10	0.21	24	85–110 mm	56	0.35	66	0.32
	110–130 mm	7	0.29		110–130 mm	4	0.49	11	0.34
	Total	110	0.24		Total	144	0.41	254	0.32
14–18 Dec 92	45–60 mm	15	0.11	15–19 Feb 93	45–60 mm	—	—	15	0.11
	60–70 mm	39	0.27		60–70 mm	—	—	39	0.27
	70–85 mm	20	0.21		70–85 mm	52	0.28	72	0.25
30	85–110 mm	13	0.27	29	85–110 mm	38	0.24	51	0.25
	110–130 mm	4	0.17		110–130 mm	2	0.24	6	0.19
	Total	91	0.20		Total	92	0.26	183	0.23
11–15 Jan 93	45–60 mm	24	0.17	15–19 Mar 93	45–60 mm	—	—	24	0.17
	60–70 mm	23	0.16		60–70 mm	—	—	23	0.16
	70–85 mm	20	0.21		70–85 mm	19	0.10	39	0.14
34	85–110 mm	6	0.12	34	85–110 mm	19	0.12	25	0.12
	110–130 mm	6	0.25		110–130 mm	1	0.12	7	0.22
	Total	79	0.18		Total	39	0.11	118	0.15

Table 5 (continued)

Collection date (weeks after release)	Size at release	Total recap. *n*	% recapt.	Collection date (weeks after release)	Size at release	Total recap. *n*	% recapt.	Grand total	Grand total % recap.
Spring release				**Summer release**					
15–19 Feb 93	45–60 mm	19	0.14	12–16 Apr 93	45–60 mm	—	—	19	0.14
	60–70 mm	36	0.25		60–70 mm	—	—	36	0.25
	70–85 mm	23	0.24		70–85 mm	12	0.06	35	0.12
39	85–110 mm	6	0.12	38	85–110 mm	4	0.03	10	0.05
	110–130 mm	5	0.21		110–130 mm	1	0.12	6	0.19
	Total	89	0.20		Total	17	0.05	106	0.13
15–19 Mar 93	45–60 mm	5	0.04						
	60–70 mm	13	0.09						
	70–85 mm	4	0.04						
45	85–110 mm	1	0.02						
	110–130 mm	2	0.08						
	Total	25	0.06						
12–16 Apr 93	45–60 mm	2	0.01						
	60–70 mm	8	0.06						
	70–85 mm	3	0.03						
47	85–110 mm	—	—						
	110–130 mm	—	—						
	Total	13	0.03						
Totals	45–60 mm	195	1.39	Totals	45–60 mm	—	—	195	1.39
(weeks 3–39)	60–70 mm	453	3.19	(weeks 3–38)	60–70 mm	—	—	453	3.19
	70–85 mm	373	3.90		70–85 mm	650	3.44	1,023	3.60
	85–110 mm	185	3.83		85–110 mm	631	4.00	816	3.96
	110–130 mm	80	3.35		110–130 mm	37	4.51	117	3.64
Grand totals (through week 39)		1,286	2.86			1,318	3.72	2,604	3.23

earlier studies with July releases; and 2) the late-summer decline in abundance resulted in less reduction in release impact in 1992 than in other years.

Recapture rates were disproportionately higher in this study than after releases in 1990 and 1991 (Table 6). Number of fish released at Kahaluu Stream in 1992 exceeded the number released at that same site in 1990 and 1991 by 690% and 180%, respectively. Yet the total number of fish recaptured from week 16 on exceeded comparable data (similar sampling effort) from 1990 and 1991 by 1,560% and 420%, respectively (Table 6). Increase in the effectiveness of 1992 releases is revealed by comparing recapture frequencies (no. recaptured/no. released) and by including data from all release sites. From week 16 on, 1.65% of the cultured mullet released in 1992 were recaptured in cast-net samples. This recapture rate was 6 times that seen in the 1990 study (0.28%) and 1.7 times the rate in the 1991 study. Sampling frequency and number of cast-net samples were nearly identical among the three studies.

These differences among studies were statistically significant. Recapture rates after 1992 releases were significantly greater than expected in all pair-wise comparisons of 1992 data with data from 1990 and 1991 (Table 6; *G*-tests, $P<0.001$ in all cases). The 1991 study yielded significantly greater recapture rates than did the 1990 study, when fish released outside of the Kahaluu site in 1990 are included in the comparison (Table 6; all sites, $\chi^2 = 225$, $P<0.001$).

Discussion

Marine enhancement potential

Context of this study A rigorous test of marine stock-enhancement involves several phases of research. These are considered here to place the current study in perspective. Key research phases include 1) understanding both wild stock distribution

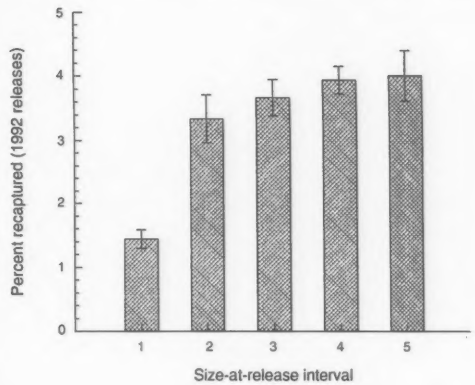

Figure 5

Recapture frequencies ([number recaptured/number released] × 100% [±SEM]) of cultured striped mullet juveniles released in 1992 and subsequently collected over 11 months at four nursery habitats in Kaneohe Bay. Combined data for fish from both spring and summer releases (n=6 lots) are presented and compared over the five size-at-release intervals: interval 1 = 45–60 mm, 2 = 60–70 mm, 3 = 70–85 mm, 4 = 85–110 mm, and 5 = 110–130 mm total length.

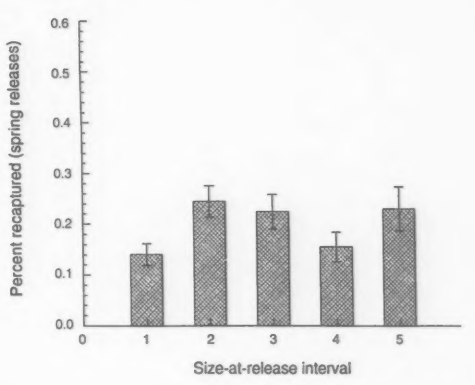

Figure 6

Recapture frequencies ([number recaptured/number released] × 100% [± SEM]) following spring releases (n=3 lots) of cultured striped mullet juveniles in 1992. These are combined data from four nursery habitats sampled in Kaneohe Bay. Data are plotted against size-at-release intervals, which are explained in the legend for Figure 5. Data are for the period from 16 weeks after release through the end of the study.

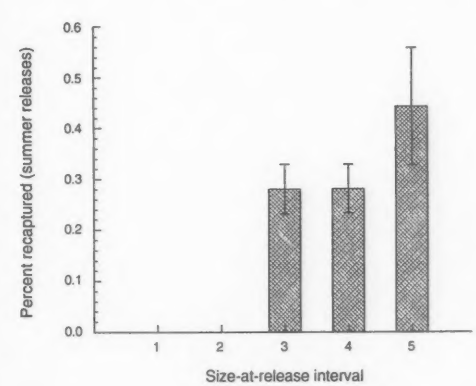

Figure 7

Recapture frequencies ([number recaptured/number released] × 100% [± SEM]) following summer releases (n=3 lots) of cultured striped mullet juveniles released in 1992. Size-at-release intervals are explained in Figure 5. No fish in the two smallest intervals were released in summer 1992. Data from the four nursery habitats are combined and are for the period from 16 weeks after release through the end of the study.

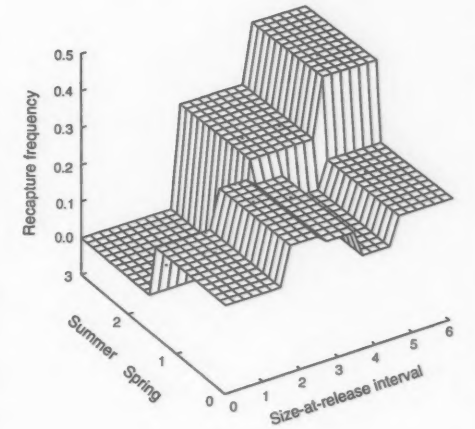

Figure 8

Comparison of spring and summer recapture frequencies of cultured striped mullet for the period from 16 weeks after release through the end of the study. No fish in the two smallest size intervals were released in summer. Data from the four nursery habitats are combined. Size-at-release intervals are explained in Figure 5.

and abundance patterns as well as behavior and ecological interactions; 2) conserving wild stock genetics and health; 3) developing reliable culture techniques; 4) establishing and testing a tagging method to identify hatchery fish; 5) evaluating optimal release strategies through experimentation; 6) assessing hatchery-release effect on population size and fishery landings; and 7) modeling economic costs and benefits (Richards and Edwards, 1986; Shaklee et al., 1993). These issues are interrelated to some degree (Blankenship and Leber, 1995).

That cultured fish will survive in the wild and contribute to stock abundance is a basic assumption that should be tested early in the development stage of planned hatchery-release programs (Richards and Edwards, 1986), notwithstanding the need to consider fish genetics and health, as well as economics of the fishery. In coastal ecosystems, understanding the potential of stock enhancement involves at least four levels of investigation in order to quantify growth

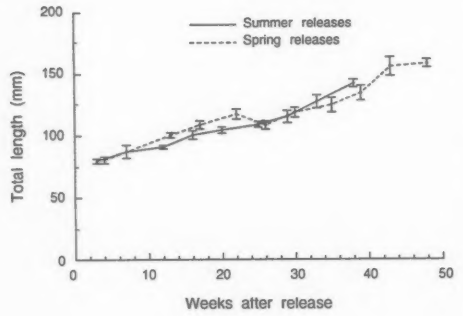

Figure 9

Mean total length (±SEM, n=3 lots) of cultured striped mullet released at 70–85 mm TL in spring and summer 1992 and retrieved in net samples over the next 10 to 11 months.

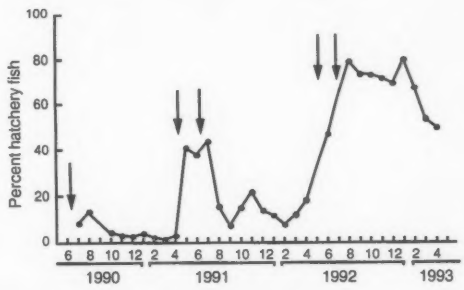

Figure 10

Percent contribution of cultured striped mullet to total abundance (wild and cultured striped mullet) in cast-net samples over a three-year study period in Kaneohe Bay (including this study). Data are from monthly cast-net collections at Kahaluu Stream. Arrows identify release periods. Spring and summer releases were conducted in 1991 and 1992. Releases in 1990 were made only in summer. Numbers on x-axis represent months of the year.

Table 6

Summary of numbers of cultured mullet released and recapture frequencies in Kaneohe Bay following hatchery releases in 1990, 1991, and 1992. Chi-square values (χ^2) and probablity levels (P) from G-tests are given for pair-wise comparisons of recapture frequencies (1990 vs. 1991 and 1991 vs. 1992). There were two release sites in Kaneohe Bay in 1990 and 1991.

	Kahaluu Stream			All sites combined		
	1990	1991	1992	1990	1991	1992
Released						
Total tagged	11,676	45,790	80,507	42,822	91,245	80,507
Recaptured						
Total	177	952	2,632	227	2,405	2,632
% recovered	1.52	2.08	3.27	0.62	2.64	3.27
χ^2	16.0	148		689	56	
P	<0.001	<0.001		<0.001	<0.001	
Total after 16 wk	85	315	1,326	118	890	1,326
% recovered	0.73	0.69	1.65	0.28	0.96	1.65
χ^2	0.021	225		225	147	
P	>0.640	<0.001		<0.001	<0.001	

and survival of cultured fish in the wild, each focused on different life stages:

Level 1 ***Initial recapture rate:*** A key issue is whether a release-recapture design is adequate to evaluate stocking effectiveness. Initial sampling of released fish after a pilot release (e.g. during the first couple of months) will establish whether monitoring is feasible under the chosen release strategies (e.g. release habitat, fish size at release) and with the condition of released fish and sampling design. An early look at recapture rates reveals a maximum expected recapture rate for a particular release (which will likely decrease over time because of mortality and dispersal) and can help determine whether release strategy or sampling strategy needs to be redesigned.

Level 2 ***Growth, survival and impact on abundance through the nursery stage of the life cycle:*** Assessing comparative effectiveness of release strategies in increasing juvenile recruitment can provide an early indication of enhancement potential. Two corollaries of the enhancement concept should be considered here: the first—cultured fish survive, grow, and contribute to population size—cannot be evaluated meaningfully without information on how chosen release strategies affect postrelease survival; the second corollary—cultured fish do not displace wild stocks—can be evaluated experimentally, once dispersal patterns are understood (Leber et al., 1995).

Level 3 ***Growth, survival, and release impact through asymptotic growth:*** involves assessment of release impact on adult population size and fishery landings. Recapture rates and growth can also be modeled to evaluate enhancement potential (Polovina, 1990, 1991). Results gained at level 2 on release-strategy impacts on survival may need to be confirmed at this level (e.g. a collecting gear bias favoring smaller fish can mask a size-at-release impact on survival at level 2; Leber et al., in press; Leber and Arce, in press).

Level 4 ***Impact on reproduction and recruitment in subsequent generations:*** With genetic markers to track hatchery impact across generations, an assessment can be made of hatchery impact on production of the next generation (Jørstad et al., 1994a).

Criteria for success need to be specified as testable hypotheses in enhancement programs (Larkin, 1979; Peterman, 1991; Blankenship and Leber, 1995). Percent increase in fish population size needed for success will depend on fish species and enhancement objectives. Cost-benefit evaluations can help determine yields required to break even. But value can be subjective and difficult to quantify when the objective is to enhance a recreational fishery or a threatened or endangered species. We evaluated success in terms of impact on recruitment and improvement in recapture rate in this study compared with our earlier studies. Our data reveal how information from pilot studies can be used to identify effective release strategies. Break-even costs for striped mullet enhancement are considered elsewhere (Leber and Cantrell[5]).

Enhancement concept with striped mullet In this paper, we address level 2 above and reveal a substantial hatchery contribution in nursery habitats following releases of cultured mullet. Results of this study corroborate the first corollary of the marine stock enhancement concept, that released fish can survive, grow, and contribute to recruitment. Released juveniles integrated with wild mullet at primary nursery habitats in Kaneohe Bay. Cultured mullet were abundant in samples on every collection date over the 11 months. Cultured fish showed linear growth; those released in May 1992 doubled in size within 48 weeks, with growth rates similar to wild striped mullet (Leber et al., in press). The second corollary, that cultured mullet are not displacing wild mullet at the Kahaluu Stream release site, was experimentally evaluated and corroborated in a follow-up field experiment (Leber et al., 1995).

Hatchery effect on abundances in nursery habitats was remarkable after adjusting release strategy to incorporate findings from pilot releases in Kaneohe Bay. Except for anadromous fishes, there are very few examples where hatchery releases have revealed the potential to double juvenile recruitment success with a marine organism (e.g. Kristiansen and Svåsand, 1990, for cod; Kitada et al., 1992, for flounder; Honma, 1993, for scallops). Cultured fish released in this study increased recruitment of juvenile striped mullet at the release site in 1992 by at least 100%. This large effect was partly a function of a poor recruitment year for wild fish and was partly due to higher survival following summer releases, compared with survival in earlier studies (Leber, 1995; Leber et al.[3]). Release impact on abundance

[5] Leber, K. M., and R. N. Cantrell. 1996. Effect of fish size-at-release on the relative cost to enhance striped mullet in Hawaii. In review.

was also considerable in streams 3 km away from the release site. Decrease in proportions of cultured fish in samples after 8 months coincided with the seasonal period (March) when yearlings begin to move out of nursery habitats into deeper water and when new recruits begin to arrive (Major, 1978; Leber, 1995; Oceanic Institute[4]).

The striped mullet collected in this study that were released in 1991 (Leber et al.[3]) represented a large portion (28%) of the total striped mullet caught in net samples at Kaneohe Stream. These data document that a portion of the cultured striped mullet released in Kaneohe Bay can be found in their nursery habitats up to two years after release.

It is evident from this study and from follow-up creel interviews in which fishery landings were surveyed that there is significant potential to increase the striped mullet population in Kaneohe Bay with relatively small-scale hatchery releases. Cultured mullet released in spring 1992 were first detected in the commercial fishery in Kaneohe Bay in October 1993, when a 367-mm-TL fish was recovered during contact interviews with commercial fishermen (Leber and Arce, in press). By the seasonal closure of the fishery in December 1994, 119 of the mullet released in 1992 had been recovered through contact interviews with commercial fishermen. According to tag data from interviewing fishermen in Kaneohe Bay, fish released in this study accounted for 9% of the commercial catch during fall 1994, at which time the proportion of cultured fish to wild fish was increasing logarithmically. Ninety-four of the cultured fish caught were checked for maturity; 44 males were ripe with milt and 2 females were gravid with mature eggs (Leber and Arce, in press).

Survival and hatchery impact on abundance The best gauge of the immediate effect of the 1992 hatchery releases on mullet population size is actual abundance of released fish in the wild. But actual number of survivors after 11 months is unknown. The >50% hatchery contribution to abundance at the release site is impressive, but from an economic viewpoint, data on actual increases in yields and population size are needed to compare the benefits of enhancement with costs. An estimate of survival would be a better gauge of stock-enhancement impact than would the proportion of hatchery fish in the population.

However, it is logistically difficult to quantify actual survival of released cultured fishes in open coastal environments. There is substantial literature on evaluating animal survival, much of which is based on change in relative abundance (catch per unit of effort [CPUE]) over time in mark-release-recapture experiments. The analysis theory for release-recapture experiments dates back to Ricker's (1945, 1948) relative recovery-rate method. A more general theory based on maximum likelihood was developed independently by Seber (1970) and Youngs and Robson (1975). Brownie et al. (1985) and Burnham et al. (1987) have provided a detailed discussion of maximum-likelihood methods. These methods for estimating survival are based on change in abundance in samples over time and are confounded in open environments by dispersal into and out of the population (Connor et al., 1983; MacCall, 1990; Nichols and Pollock, 1990; Frank, 1992) and by gear bias, as capture probabilities change with changes in fish size and habitat selection (e.g. Kjelson and Colby, 1976; MacLennan, 1992; Thompson, 1994; Acosta and Appeldoorn, 1995; Leber et al., in press). Without reliable estimates of immigration and emigration, one can use change in capture rate over time to measure loss from a population (i.e. the sum of mortality + emigration) but not to estimate mortality alone.

In this study, decrease in abundance over time in cast-net samples is a poor indicator of actual survival. Striped mullet move out of their nursery habitats as they approach maturity (Blaber, 1987), and juveniles move from shallow water to deeper water during their first year (Major, 1978; Leber et al.[3]). Overall decline in mullet abundance in samples over the 11-month study period was due to a combination of mortality, dispersal, and gear bias as mullet grew and moved into deeper water where cast nets are not effective sampling devices.

Postrelease mortality prior to initial sampling is also a source of error in estimating survival following hatchery releases. A key question is whether mortality of cultured fish is intense during the first day or so after a release (e.g. what percent of released individuals are consumed by predators?). Initial mortality could be an important factor in enhancement dynamics and should be accounted for in survival estimates, especially in open environments where mortality can be confused with emigration. But initial postrelease mortality has received little attention in "release-recapture" literature. There is evidence, however, that until cultured fish have been conditioned by exposure to predators in the wild, inadequate predator avoidance behavior can result in increased mortality (Parker, 1968; Healey, 1982; Olla and Davis, 1988; Olla and Davis, 1989; Tsukamoto, 1993; Olla et al., 1994). Initial mortality following hatchery releases of Pacific salmon can be severe and is most intense during the 48-h period following releases.[6] Ini-

[6] Blankenship, H. L. 1995. Washington Department of Fish and Wildlife, 600 Capitol Way North, Mail Stop 43149, Olympia, WA. Personal commun.

tial behavior of stocked fish can also be directly affected by handling stress and temperature change, either of which could cause an increase in susceptibility to predators shortly after release (Fuiman and Ottey, 1993).

The difficulty in quantifying initial mortality is in obtaining an unbiased early sample of abundance to establish a baseline recapture rate for comparison with recapture rates in later samples. Dispersal of striped mullet from the point of release is not an immediate event (Leber et al., personal observ.). The first few hours after a release should be the very time when released fish are most vulnerable to predators. However, immediate sampling in an open environment to determine initial abundance in samples violates assumptions of basic mark-recapture models (Ricker, 1975), primarily the assumption that marked fish mix randomly within the study area.

Without a reliable, unbiased method to estimate postrelease survival in open coastal ecosystems, how do we gauge benefits from hatchery releases? In effect, the best indicator of hatchery impact is total annual catch of cultured fish in a fishery. Thus, assessment of marine stock enhancement requires unbiased estimates of CPUE, total fishing effort, and proportion of cultured fish in the fishery. Accurate catch statistics for marine organisms are expensive and often lacking (e.g. Shomura[7]), as in Hawaii for striped mullet. The difficulty of assessing total hatchery impact is exacerbated when cultured fish are released unmarked, which has often been the case with marine fishes (discussed in Richards and Edwards, 1986).

Because a fishery on juveniles is lacking, some measures besides fishery landing statistics are needed to evaluate survival of cultured fish during the nursery phase. Consequently, researchers in coastal systems report recovery rates and percent cultured fish in samples of cultured and wild fish (hatchery contribution) as early indicators of enhancement effect. Percentage of cultured fish can be a good relative indicator of release impact but only when reported with CPUE for wild and cultured fish. Hatchery contribution is a function of abundance of wild fish, release magnitude, survival, dispersal, size of hatchery and wild fish, and environmental carrying capacity.

Hatchery contribution is sensitive to variation in any of the above six factors. Thus, alone, it has low information content as an indicator of success. In fact, year to year comparisons of hatchery contribution can be misleading. Three examples below illustrate the relationship among hatchery contribution (%C), CPUE of cultured (C) and wild fish (W) in samples, and actual hatchery effect on recruitment:

Example 1 %C in year 1 and year 2 are equal, but W is greater in year 2: hatchery effect on magnitude of recruitment actually increased; increase is not apparent from comparing %C but is when C and W are compared between years;

Example 2 %C is greater in year 2 but W is less: actual hatchery effect on abundance could be identical in years 1 and 2;

Example 3 %C and W are both greater in year 2: substantial increase in hatchery effect (i.e. greater hatchery impact than realized by merely comparing %C between years).

Lacking an unbiased indicator of actual survival following hatchery releases, we submit that recruitment, hatchery contribution, and recovery rate (no. captured/no. released) provide a good preliminary indication of enhancement effect if all three of these are presented. Each is needed to evaluate and control enhancement effectively.

Variation in fishery yields is driven largely by recruitment dynamics (see Frank and Leggett, 1994, for recent review). The CPUE of cultured and wild fish reflects the magnitude of recruitment, which should have a direct relevance to fishery yields, if food and habitat are available. Also, without CPUE data, there is no indication of how the whole population (cultured and wild individuals) is changing from year to year in response to natural recruitment processes, enhancement, and other management strategies.

Hatchery contribution from pilot studies can be used as an index to help in planning release magnitude at levels that would not swamp wild stocks with cultured fish. Hatchery contribution is easily computed from CPUE data (i.e. $\%C = [C \times 100\%] / [C + W]$).

Because cost effectiveness is directly related to survival of cultured fish in the wild, optimizing recovery rate should also be a key consideration in enhancement programs (Kitada et al., 1992). Recovery rate provides a relative measure of survival and is a good indicator (if standardized by sampling effort) for comparing performance of cultured fish. In comparisons of recovery rates from different years, differences in release magnitude are factored out.

The above three indicators can be used to evaluate release effects during the juvenile stage, before fish enter the fishery, to obtain a preliminary estimate of stock enhancement success. Thus, a way of

[7] Shomura, R. S. 1987. Hawaii's marine fishery resources: yesterday (1900) and today (1986). Honolulu Laboratory, Southwest Fisheries Center, Natl. Mar. Fish. Serv., Admin. Rep. H-87-21.

characterizing field data is needed that clearly reflects 1) recruitment (CPUE) of both cultured and wild fish, 2) hatchery contribution, and 3) standardized recovery rates for released fish. One way of illustrating these variables together is presented here.

All three indicators are used in Figure 11 to compare relative hatchery effect at Kahaluu in 1992 with data from three other years of pilot releases (Leber, 1995; Leber et al., 1995; Leber et al.[3]). Overall, CPUE of cultured juveniles was greatest after 1992 releases. However, recovery rate (and presumably survival) was greatest after 1993 releases. Thus, 1992 releases had greatest impact on recruitment, whereas yield per stocked juvenile was greatest from 1993 releases. Recovery rate improved in 1992 and again in 1993. The improvement was largely due to better survival after adjusting SAR protocol to avoid summer releases of fish <70 mm TL and to avoid release sites outside of habitat preferred by striped mullet. Although hatchery contribution was inflated in 1992 because of reduced recruitment of wild fish, overall effect from releasing cultured fish was greatest following 1992 releases, and recovery rate improved most in 1992.

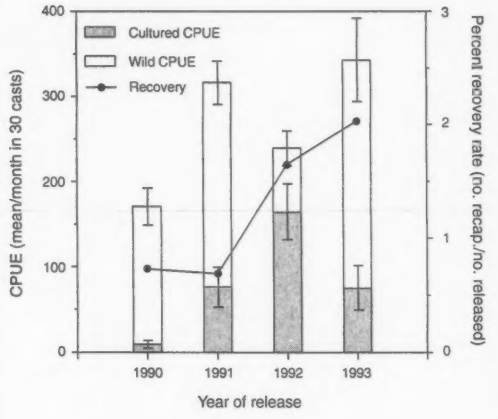

Figure 11

Stacked bar graph of release impact at Kahaluu Stream following releases conducted there from 1990 to 1993. CPUE is total number of cultured fish (gray bars) and wild fish (open bars) in 30 casts per month averaged over 10–11 monthly collections. Percent cultured fish (hatchery contribution) varied from monthly average of 4.4% (SEM =±1.3) of the striped mullet collected in 1990 to 20.6% (±4.1) in 1991, 65.2% (±5.2) in 1992, and 23.5% (±5.0) in 1993. Percent recovery rate of cultured fish (solid line with closed circles) is number recaptured/number released, × 100%.

Pilot releases

Whereas actual survival of cultured fish may be difficult to quantify in open ecosystems, relative survival can be quantified and compared across treatment groups in pilot release experiments (Burnham et al., 1987). Results from two previous years of pilot releases were used to identify optimal release strategies for this study. Discontinuing releases near the Hawaii Institute of Marine Biology (HIMB) pier after 1990 resulted in a >300% increase in recovery rate in the 1991 study; the increase in recovery rate was compounded in 1992 by modifying SAR protocol as well (Table 6; note the 1990 data in Fig. 11 are only for fish released at Kahaluu). By confining releases in this study to the vicinity of Kahaluu Stream and by adjusting minimum SAR upwards to include only fish >70 mm TL in summer, we achieved a 590% increase in recovery rate over the 1990 study and a 170% increase over the 1991 study (Table 6: after 16 weeks, all sites combined).

This study provided new information on effects of release site. Choice of release microhabitat at Kahaluu (inlet and upstream lagoon) affected dispersal north from Kahaluu into other streams but had no apparent impact on survival. The similar survival was surprising, given the poor survival in 1990 of fish released along the shoreline near HIMB pier, in comparison to fish released at streams (Leber, 1995; Leber and Arce, in press). We hypothesize that refuge from predators, afforded by mangroves and other shoreline vegetation in the north end of Kaneohe Bay, accounted for the higher survival of mullet that were released at Kahaluu Inlet and that dispersed along the shoreline.

Release microhabitat affected the extent of enhancement in Kaneohe Bay in this study by partially controlling colonization of nursery habitats north of Kahaluu. If a management objective for full-scale releases were to have a portion of fish from each release lot disperse into adjacent nursery sites in the bay (e.g. in order to maximize use of available nursery habitat), then releases at the inlet to Kahaluu Stream would achieve this. If stronger site fidelity were desired, releases farther upstream would result in lower dispersal during the nursery phase of the life cycle. The ability to affect which nursery habitats are selected by released fish, coupled with knowledge about recruitment success of wild fish, could be used to help prevent overstocking a particular nursery.

Implications

This study shows that information from pilot releases is critical for managing full-scale stock enhancement

in coastal environments. The use of results from pilot studies to modify release protocol caused a considerable increase in recovery rates and hatchery contributions to striped mullet abundance in their nursery habitats. Even before fish enter a fishery, data on relative survival of juveniles following pilot releases can be used to design effective release strategies.

The results of this study could be magnified if enhancement activities expanded to include other nursery sites in Kaneohe Bay, provided sufficient habitat is available. Leber et al. (1995), reported hatchery releases of cultured striped mullet at Kahaluu had an additive effect on population size. Kahaluu, Kaalaea, and Waiahole streams are primary mullet nursery habitats in Kaneohe Bay; including the latter two with Kahaluu as release sites would increase stock-enhancement effect.

According to this study, Leber et al. (1995), and Leber and Arce (in press), marine stock enhancement appears to have high potential as an additional fishery management tool for Hawaiian coastal fishes. Hatchery releases of striped mullet could be used in conjunction with fishing regulations and habitat protection, with the expectation that recruitment success of juveniles and subadults would increase significantly in Kaneohe Bay. To ensure that stocks are actually enhanced by hatchery-release activities, information from pilot studies needs to be coupled with additional management considerations to provide a controlled approach to stock enhancement (Peterman, 1991; Cowx, 1994; Blankenship and Leber, 1995).

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Abstract.—Kelp bass, *Paralabrax clathratus,* and barred sand bass, *P. nebulifer,* are major components of the nearshore marine environment in the southern California Bight. Both species are also very important parts of the marine recreational fishery. Surveys at King Harbor, Redondo Beach, California, have shown that kelp bass primarily recruit between August and December. In general, both kelp bass and barred sand bass numbers increased in King Harbor beginning in the late 1970's and continuing into the 1980's. Male and female kelp bass and barred sand bass grow at the same rates, and growth rates of both species are similar. The oldest kelp bass in our sample was 33 yr old, the oldest barred sand bass was 24 yr old. For kelp bass, 50% of males matured at 22.0 cm; for barred sand bass, 50% of males matured at 21.9 cm. For kelp bass, 50% of females matured at 22.6 cm; for barred sand bass, 50% of females matured at 23.9 cm. In both species, males matured between ages 2 and 4 years and females matured between ages 2 and 5 years.

Aspects of the life histories of the kelp bass, *Paralabrax clathratus,* and barred sand bass, *P. nebulifer,* from the southern California Bight

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Kelp bass, *Paralabrax clathratus,* and barred sand bass, *P. nebulifer,* are major components of the nearshore marine environment in the southern California Bight.

Kelp bass grow to 72 cm total length (TL) and occur between the mouth of the Columbia River, Washington, and southern Baja California, most commonly from Point Conception, California, southward (Eschmeyer et al., 1983). Distributed from intertidal waters to 59 m (Quast, 1968), most fishes live in 3–25 m (Feder et al., 1974). Although usually associated with substrata, kelp bass will often rise into the water column, well away from structure.

Barred sand bass reach 65 cm (TL) and range from Santa Cruz, central California, to southern Baja California (abundant from Pt. Conception southward). This species is distributed from subtidal water to 183 m (Eschmeyer et al., 1983). Barred sand bass are benthic, relatively sedentary fish which, in contrast to kelp bass, are rarely found more than 3 m above the substratum (Turner et al., 1969; Feder et al., 1974; Larson and Demartini, 1984).

Both species are very important parts of the marine recreational fisheries of southern California and northern Baja California (Rodriguez Medrano, 1993; Ally et al.[1];

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Love et al.[2]). Measured by catch per unit of effort, both species rank annually among the top three species in the commercial passenger fishing vessel catch (Love et al.[2]).

The life histories of these two species are poorly understood. While there is some information on habitat preferences, food habits, and reproduction, summarized in Read (1992) and Ono (1992), data on age and growth as well as size and age at first maturity and recruitment are limited. We describe the age and growth patterns and size and age at first maturity relationships for kelp bass and barred sand bass in the southern California Bight. In addition, we provide information on recruitment of kelp bass to a nearshore southern California reef.

Methods

Recruitment and annual abundance

Since 1974, we have used 5-min isobathic diver transects at 3-m depth intervals between 1.5 and 15 m at 8 stations along the breakwater in King Harbor, Redondo Beach, California (Fig. 1) to estimate fish abundance by life history stage. During these transects, divers swam along the vertical face and counted all fishes in a 3-m deep band (1.5 m above and below the diver). Outer harbor transects were 254 m in length, inner ones were 208 m long. Transects were swum monthly in 1974 and 1975 and quarterly after 1976. For the years after 1975, this survey yielded 96 transects per year (8 stations and 3 depths surveyed quarterly).

We obtained data on month of recruitment for kelp bass from 1986 to 1992 by conducting a monthly survey along the inner wall of the Redondo Beach breakwater and along a rock groin within the inner harbor. Three divers (at depths of 0–3, 4–6, and 7–10 m) swam parallel transects along approximately 500 m of rock and closely inspected bottom cover, crevices, and algae for newly settled fishes (Pondella and Stephens, 1994). The survey along the inner rock groin was similar, except that only two divers swam transects (one shallow, one deep), because of the shallower (1–4 m) location. Fishes ranging from 1.5 to 2.0 cm were considered newly recruited. Juveniles were considered to be those fish from 2.1 to 10.0 cm, and subadults ranged from 10.1 to 15.0 cm. Barred sand bass do not recruit from the plankton to the rocky substrate of King Harbor.[3]

Age and growth

Between 1978 and 1992, we collected kelp and sand bass throughout southern California waters by using hook and line as well as pole spear. These samples were supplemented by fish from commercial passenger fishing vessel (CPFV) catches, from kills at coastal power plant intakes (water heat treatments), from experimental gill-net studies, and from California Department of Fish and Game wardens. Data collected from all fishes included total length, sex, capture location, and collection date. We ascertained whether the fish were mature or not by an inspection of their gonads during spawning season. We also collected otoliths from each fish. In cases where standard lengths were recorded, we converted these to total lengths by using length conversions (Table 1).

Otoliths were embedded in plastic and sectioned prior to being read. We made an embedding mold from 3/4-inch pvc pipe with stoppered ends, cut in half longitudinally. A thin layer of resin (1/4 inch thick) was poured into the mold and allowed to harden. The otoliths were then placed into the mold with a label containing an identification code and

[2] Love, M. S., A. Brooks, and J. R. R. Ally. 1996. An analysis of the commercial passenger fishing vessel fisheries for kelp and barred sand basses (*Paralabrax clathratus* and *P. nebulifer*) in the southern California Bight. In review.

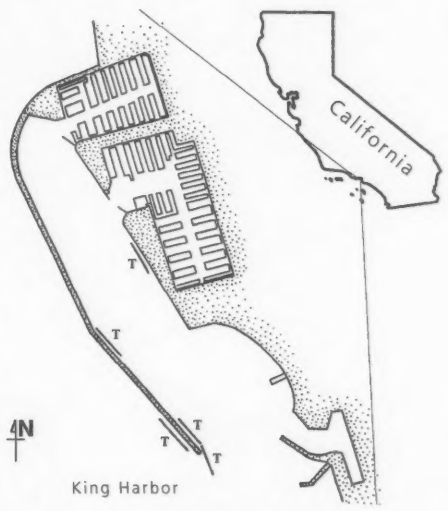

Figure 1
Location of underwater transect sites (marked with a "T"), King Harbor, Redondo Beach, California.

[3] Pondella, D. 1995. Department of Biology, Occidental College, 1600 Campus Rd., Los Angeles, CA 90041. Personal commun.

Table 1

Conversions between standard (SL), fork (FL), and total lengths (TL) for kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) (each species, n=100). [As an example, to calculate the total length of a kelp bass of 20.0 cm standard length: $TL = b + m(SL)$ = 1.41 + 1.20 (20.0) = 24.1 cm.] Maximum and minimum total lengths used in the these analyses were as follows: kelp bass, 12.7 and 48.5 cm; barred sand bass, 17.8 and 49.4 cm.

	r^2
Kelp bass	
FL = 2.38 + 1.10 SL	0.89
TL = 1.41 + 1.20 SL	0.96
TL = 0.83 + 1.01 FL	0.93
Barred sand bass	
FL = 1.11 + 1.17 SL	>0.995
TL = 0.70 + 1.22 SL	>0.995
TL = 0.46 + 1.05 FL	>0.995

covered by additional resin. After curing, the hardened resin bar was taken from the mold.

We used a Buehler Isomet saw with two low-density diamond blades separated by a thin (0.3–0.5 mm) metal shim to section each otolith. Otolith sections were placed in a 50% solution (by volume) of glycerol in water and cleaned in an ultrasonic bath for 2–3 minutes. After cleaning, sections were dried and stored in labelled plastic bags. Sections were later placed on a glass slide, cleaned with 2–3 drops of toluene, and mounted with enough cytoseal to cover the structures and ensure permanent storage.

Many fishes lay down annually an opaque and a hyaline (translucent) zone in their otoliths. Seasonal variations in calcium deposition may be responsible for this zonation (Irie, 1960). By calculating the percentage of fish with otoliths with opaque margins in our monthly samples, we attempted to validate that the bands were formed annually. It seems reasonable to assume that band deposition was seasonal if the bands were present during one part of the year. Kelp and sand bass do appear to lay down seasonal bands, beginning in spring and continuing into fall (Fig. 2). In both species, the first three annuli were usually readable. The fourth one was often more difficult to distinguish; however, bands subsequent to number four were clear.

Lengths at ages were estimated by direct observation of otolith annuli from 261 kelp bass and 137 barred sand bass. Growth was assumed to be described by the von Bertalanffy growth curve model (von Bertalanffy, 1938):

$$l_t = l_\infty\left(1 - e^{-k(t-t_0)}\right),$$

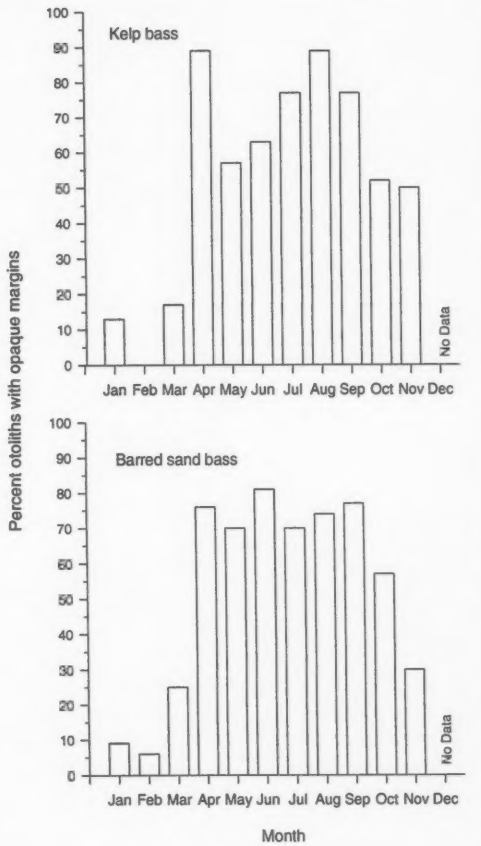

Figure 2

Seasonal deposition of opaque edges in kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) otoliths from southern California (kelp bass, n =204; barred sand bass, n=238).

where l_t = length at time t;
l_∞ = theoretical maximum length;
k = constant expressing the rate of approach to l_∞; and
t_0 = theoretical age at which $l_t = 0$.

Growth equation constants for the von Bertalanffy growth model were calculated from length-at-age data for each species by using the Marquardt method of iteration in a least-squares, nonlinear regression (SAS, 1988). We were unable to accurately fit these functions separately by sex for either species because of our relatively small sample sizes and, in particular, because of the absence of smaller-size fish that could be unambiguously sexed. We did test the hy-

pothesis that there was no difference between the growth rates of kelp bass and barred sand bass by constructing a "complete" least-squares, nonlinear regression model that fitted the three von Bertalanffy parameters t_0, l_∞, and k separately for each species. We then used an F-test to compare the amount of variance explained by this separate species model with that explained by a "combined-species model," fitting the data for both species to just one set of parameters. A nonsignificant F-value indicated that no significant additional variation was explained by assuming different values for the three von Bertalanffy parameters for each species.

Length and age at first maturity

We sampled kelp and sand bass in July–August 1988–89, July 1991, and June–August 1992. As we have noted previously in rockfishes (*Sebastes* spp., Love et al., 1990), white croaker (*Genyonemus lineatus,* Love et al., 1985), and California halibut (*Paralichthys californicus,* Love and Brooks, 1990), it is often difficult to distinguish immature from mature fishes during their nonreproductive seasons. Thus, we concentrated our sampling on the summer months, well within the spawning seasons of the two species. Most of the sand bass were taken by a 7.6-m semiballoon trawl, by hook and line, or by gill nets between Marina del Rey and San Diego. Kelp bass were taken by hook and line and gill nets between Redondo Beach and Newport Beach and at Santa Catalina and San Clemente islands. Fish were frozen until analyzed, when they were measured (TL) and both sagittal otoliths and gonads were removed. Gonads were examined without magnification to determine sex and gonad state. Annuli from otolith sections were counted under water with a dissection microscope. Sixty-eight male (16–36 cm TL) and 84 female (14–35 cm TL) kelp bass as well as 66 male (12–33 cm TL) and 85 female (13–35 cm TL) barred sand bass were examined.

The relationships between length and maturity and age and maturity were established by using a natural log transformation of the equation

$$p_x = \frac{1}{1+e^{ax+b}}$$

(Gunderson et al., 1980) to yield

$$\ln\frac{(1-1)}{p_x} = ax+b,$$

where p_x is the proportion mature at length or age x, and a and b are fitted parameters. We then plotted x against

$$\ln\frac{(1-1)}{p_x}$$

using simple linear regression (SAS, 1988) to estimate values for a and b. Fifty-percent maturity was calculated by using fitted values of a and b, and by using $p_x = 0.50$ to solve for x.

Results

Recruitment and annual abundance

Kelp bass showed considerable seasonal variation in recruitment at the King Harbor breakwater (Fig. 3). A few newly settled recruits were found in April, more in May, but most were observed during transects conducted in the fall and winter. Surveys of young of the year (YOY), subadult, and adult kelp bass in King Harbor showed a distinct temporal pattern (Fig. 4). Low in the mid-1970's, YOY abundance increased sharply from 1977 to 1979, decreased in the early 1980's, and

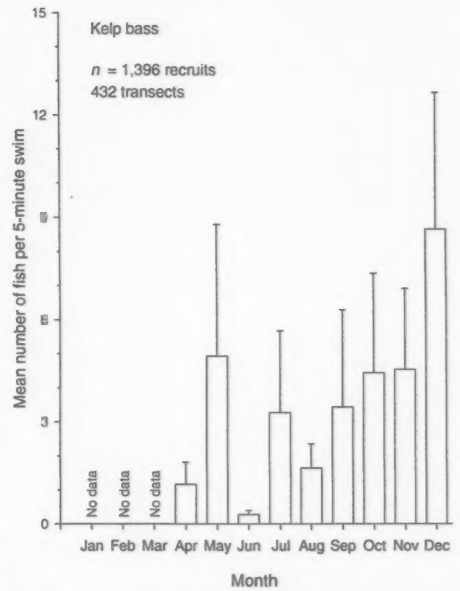

Figure 3

Monthly recruitment of kelp bass, *Paralabrax clathratus*, (1986–92) at the King Harbor (Redondo Beach, California) breakwater. We considered recruitment to any month to have occurred between the 16th day of the current month and the 15th of the next month. Means are based on monthly data from 1986 to 1990. Error bars represent ± one standard error.

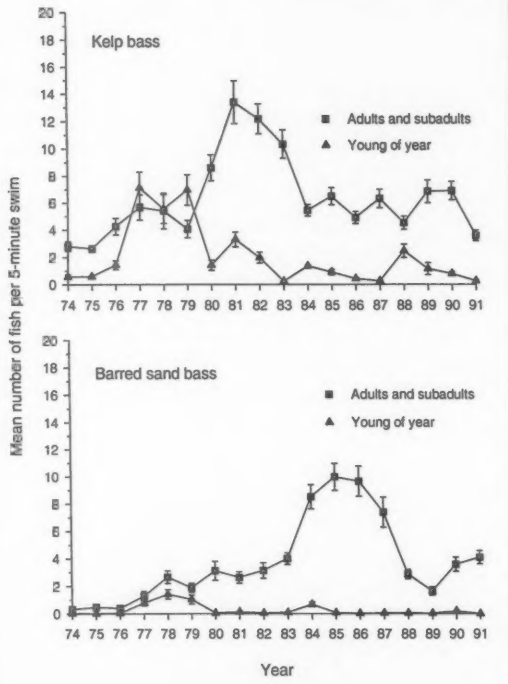

Figure 4

Mean abundance per transect of adults or subadults, or both, and young-of-the-year (YOY) kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) along the King Harbor (Redondo Beach, California) breakwater 1974–90. Error bars are ± one standard error. Each point represents mean of 96 five-minute diver surveys (8 stations and 3 depths surveyed quarterly).

remained low for the rest of the decade. The abundance of adults and subadults peaked from 1980 to 1983, probably reflecting the successful year classes of the previous few years, then declined somewhat in the mid-1980's. The abundances of barred sand bass at all life stages increased in the late 1970's (Fig. 4). Although the numbers of YOY declined soon after, the population of older fishes increased continuously, reaching a peak in 1985.

Age and growth

For each species, we combined age-at-length data for both sexes. We did this because we were unable to accurately fit the von Bertalanffy growth functions separately by sex because of our relatively small sample sizes and, in particular, because of the absence of smaller-size fish that could be unambiguously sexed. We do not feel that by combining this data undue bias was introduced into our results because the numbers of males and females comprising the combined samples were approximately equal (kelp bass, males = 86, females = 100; sand bass, males = 36, females = 55) and because the separate fits for each sex failed to show a significant difference in growth rates for either species (kelp bass, t=0.059, df=182, P>0.05; barred sand bass, t=0.004, df=87, P>0.05).

We tested the hypothesis that there was no difference between the growth rates of kelp bass and barred sand bass by constructing a "complete" least-squares, nonlinear regression model that fit the three von Bertalanffy parameters t_0, l_∞, and k, separately for each species. We then used an F-test to compare the amount of variance explained by this separate species model with that explained by a "combined-species model," fitting the data for both species to

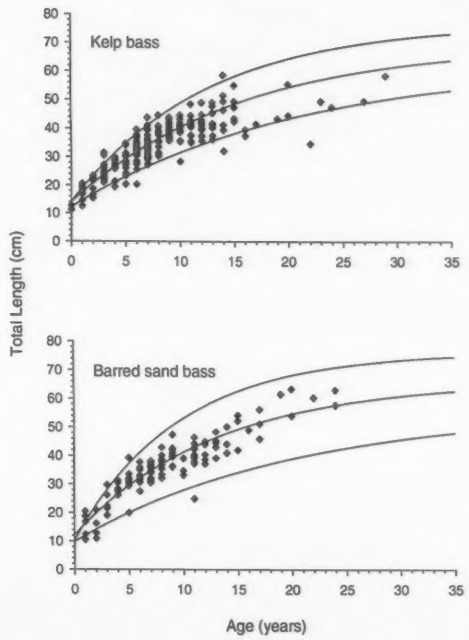

Figure 5

Von Bertalanffy growth curves for kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*) from southern California. Dotted curves are the 95% prediction limits about the von Bertalanffy regression lines.

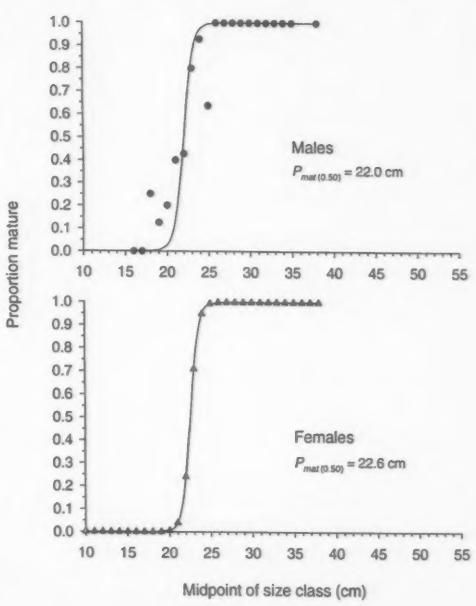

Figure 6

Length-maturity relationships for male (n=68) and female (n=84) kelp bass (*Paralabrax clathratus*) taken in the southern California Bight, including estimated lengths at which 50% of the bass were mature. Solid line represents predicted relationship.

just one set of parameters. A nonsignificant F-value ($F_{3,397}$=0.60, P>0.05) indicated that no significant additional variation was explained by assuming different values for the three von Bertalanffy parameters for each species.

In their early years, both species grew fairly quickly, a few reaching 20 cm TL in their first year (Fig. 5). Growth rates declined at around age 5. The von Bertalanffy parameters for all kelp bass (with standard errors in parentheses) were l_∞=69.8 (3.76), k=0.06 (0.008), t_0=–3.50 (0.48); those for all barred sand bass were l_∞=66.2 (5.08), k=0.08 (0.014), t_0=2.63 (0.63). The oldest kelp bass aged was 33 yr, and the oldest barred sand bass was 24 yr; however, most fish sampled were less than 15 yr old.

Length and age at first maturity

Both male and female kelp bass matured within a relatively narrow length range and at about the same age (Figs. 6 and 7). While a few males and females matured at 18 cm, 50% of males matured at 22.0 cm and 50% of females at 22.6 cm. All males were mature by 26 cm, all females by 27 cm. Males matured between the ages of 2 and 4 years; females between 2 and 5 years.

The smallest mature male barred sand bass that we found were 19 cm, the smallest females were 21 cm (Figs. 8 and 9; Table 2). All males were mature by 26 cm, all females by 27 cm. Length at 50% maturity was 21.9 cm for males and 23.9 cm for females. As with kelp bass, male barred sand bass matured between the ages of 2 and 4 years, and females between 2 and 5 years.

Discussion

Recruitment and annual abundance

In the annual recruitment pattern, kelp bass is a late spring to early fall spawner. Because this species has a pelagic larval phase lasting at least one month (Butler et al., 1982), most of this recruitment pattern would be expected. The peak of recruitment seen in December may represent an artifact of slower win-

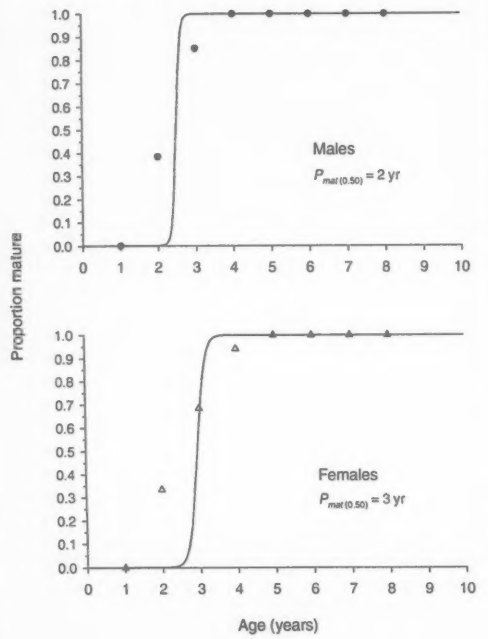

Figure 7

Age-maturity relationships for male (n=68) and female (n=84) kelp bass (*Paralabrax clathratus*) taken in the southern California Bight, including estimated ages at which 50% of the bass were mature. Solid line represents predicted relationship.

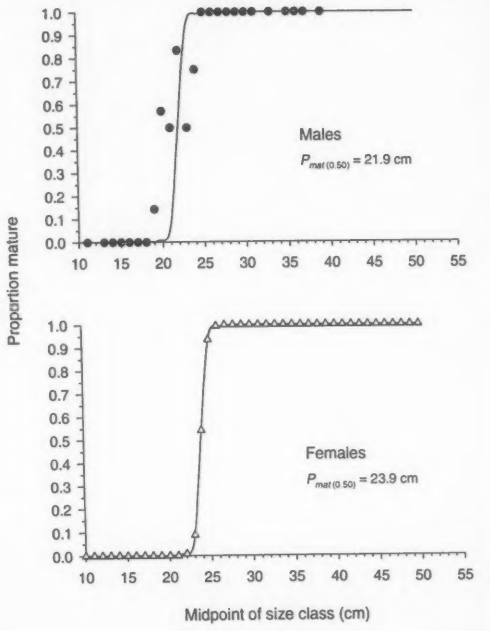

Figure 8

Length-maturity relationships for male (n=66) and female (n=85) barred sand bass (*Paralabrax nebulifer*) taken in the southern California Bight, including estimated lengths at which 50% of the bass were mature. Solid line represents predicted relationship.

ter growth rates. A fish recruited in October may not grow appreciably and, with only length as a criterion, would appear to be a new recruit in December. Barred sand bass recruitment in King Harbor was low throughout the 1980's; the large increase in numbers of older fish was probably due to immigration from outside the harbor.

We believe that the increase in abundance of kelp bass and barred sand bass in King Harbor during the late 1970's and 1980's may be related to a general warming trend of southern California waters during the period (Stephens et al., 1994). A significant increase in catches of both kelp and barred sand bass occurred then throughout the southern California Bight (Love et al.[2]). In fact, the increase in bass populations may have been part of a general alteration of nearshore fish populations, resulting from warming ocean waters. During this period, colder-water species (such as rockfishes) declined in abundance, whereas populations of warm-temperate and subtropical species (including labrids and pomacentrids) increased (Stephens et al., 1986). This trend has also been noted among nearshore pelagic species, such as chub mackerel (*Scomber japonicus*) and Pacific sardine (*Sardinops sagax*) (Barnes et al., 1992).

Age and growth

Although no other study of barred sand bass growth rates is available, some age-length data derived from scales, for kelp bass, have been reported in Young (1963). We compared our age-at-length estimates (from the von Bertalanffy equation) with the mean length at age calculated by Young (Table 3). Except for the very youngest and the very oldest fish, our data sets are similar, particularly at ages 4–7.

The results of our comparison of growth rates of the two species suggest that there is little difference between kelp bass and barred sand bass. We were unable to reject our "combined species" model by fitting the age and length data for both species to one growth curve in favor of our "separate" model which fits the three growth parameters separately for each species.

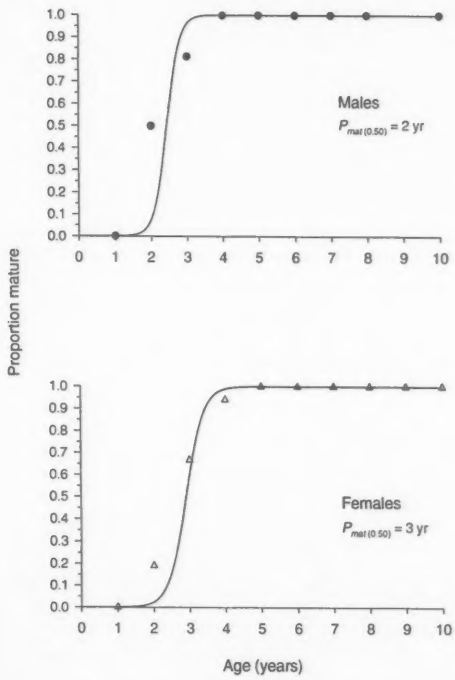

Figure 9

Age-maturity relationships for male (n=66) and female (n=85) barred sand bass (*Paralabrax nebulifer*) taken in the southern California Bight, including estimated lengths at which 50% of the bass were mature. Solid line represents predicted relationship.

Table 2

Maximum-likelihood estimates for the parameters of the logistic equation relating proportion mature to lengths and ages of kelp bass (*Paralabrax clathratus*) and barred sand bass (*P. nebulifer*). Predictive length ($l_{0.50}$) and age ($age_{0.50}$) at 50% maturity and correlation coefficients (r^2) are also presented.

	Length			
Kelp bass	a	b	$l_{0.50}$(cm)	r^2
Males	–1.77	38.88	22.0	0.65
Females	–2.04	46.03	22.6	0.59
	Age			
	a	b	$Age_{0.50}$	r^2
Males	–18.18	45.14	2.0	0.92
Females	–9.56	28.10	3.0	0.86
	Length			
Barred sand bass	a	b	$l_{0.50}$(cm)	r^2
Males	–2.48	54.49	21.9	0.67
Females	–2.50	59.82	23.9	0.68
	Age			
	a	b	$Age_{0.50}$(cm)	r^2
Males	–5.67	13.81	2.0	0.94
Females	–4.11	11.91	3.0	0.91

Table 3

A comparison of kelp bass (*Paralabrax clathratus*) age at length (to the nearest centimeter) up to age 9 in Young's study (1963) with age at length in the current study. Young's data are based on mean length at age for each year in inches and are converted to the nearest centimeter.

Age (yr)	Length (cm) Young's study (1963)	Length (cm) Current study
1	10	16
2	15	20
3	22	24
4	25	26
5	29	29
6	31	31
7	34	32
8	36	34
9	42	36

Since individuals of both species appear to be adequately described by a common age-length relationship, a comparison of size records for each species may provide some insight into their relative longevities. Eschmeyer et al. (1983) reported maximum lengths of 72 cm and 65 cm for kelp bass and barred sand bass, respectively. These lengths suggest that kelp bass may be the longer lived of the two species. Indeed, the oldest kelp bass we found was 33 yr (a new record), the oldest barred sand bass was 24 yr.

Length and age at first maturity

Clark (1933) reported on length at first maturity for kelp bass and barred sand bass taken in the commercial catch and landed at San Pedro. In that study, all kelp bass <25 cm were immature (note that she used fork length [FL]), and she assumed that the "average size at first maturity" was about 26 cm FL. We also found that there was little difference in length at first maturity for the two species. However, if we take "average size at first maturity" to mean length at which 50% of the individuals are mature,

our results are somewhat different. On average, our fish were two to four centimeters (depending on sex and species) shorter at maturity. Our results for kelp bass are very similar to those reported by Collyer and Young (1953). Clark also speculated from only a few fish that barred sand bass matured at about the same length as kelp bass.

Kelp bass and barred sand bass matured over an almost identical size and age range. In both species, sexual maturity was reached at a young age and small size, particularly when compared to many of the other large reef species in California. In the eastern Pacific Ocean, kelp and barred sand bass are the most northerly occurring Serranidae, which are typically tropical. In general, tropical fishes tend to mature at a fairly young age and these two subtropical-warm temperate species follow this pattern. The differences between these basses and some other co-occurring species, for instance the many rockfishes (Scorpaenidae) that share habitats with the two basses, is particularly pronounced. Rockfishes are typically cold-temperate species and tend to mature when older and larger, relative to maximum body length. For instance, olive rockfish (*Sebastes serranoides*), which superficially resembles kelp bass and co-occurs with it in the northern part of the southern California Bight, matures between 29 and 39 cm and between 3 and 8 years (Love and Westphal, 1981).

Conversely, the two species exhibit a typically temperate-fish growth pattern (Beverton, 1986); a relatively slow growth rate and fairly long life span. Research on a sympatric congener, the spotted sand bass, *P. maculatofasciatus*, implies that not all *Paralabrax* exhibit this pattern (Allen et al., 1995). Spotted sand bass inhabit backwaters from southern California into the Gulf of California and, compared with kelp bass and barred sand bass, exhibit a typically tropical-species pattern, with a faster growth rate and short (about 12 years) life span.

One possible explanation is that growth rate is more plastic in response to environmental conditions than is reproduction. This would lead to fishes growing more slowly, because of colder conditions in the southern California Bight, but conserving their tropically-derived reproductive schedule.

Acknowledgments

The research on kelp bass and barred sand bass age and growth, age and length at first maturity, and recreational fisheries was supported by Federal Aid for Sport Fish Restoration Program and the National Biological Service, contract number 1445-CA-0995-0386. Recruitment studies were funded through a grant from the Southern California Edison Company. Dan Pondella supplied data on abundance of kelp bass and barred sand bass recruits.

Larry Allen provided many of the specimens for this study and both he and Chuck Valle critically reviewed drafts of the manuscript. We would like to thank the crew of the RV *Yellowfin*, Jim Cvitanovich, Paul Irving, and Danny Warren, for their good-humored assistance. Michael Franklin, Tom Grothues, Tim Hovey, Ron Klaver, Loretta Roberson, Bob Scott, and Carrie Wolfe collected, prepared, and analyzed many of the fish.

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Marine distribution and origin of prerecruit chinook salmon, *Oncorhynchus tshawytscha*, in southeastern Alaska

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Abstract.—Chinook salmon, *Oncorhynchus tshawytscha*, <71 cm total length, are typically not retained in directed marine fisheries of southeastern Alaska because of size restrictions; consequently, little is known of the origin or temporal and spatial distribution of these prerecruits. To obtain such data, commercial power trollers were chartered to fish for small chinook salmon with small hooks and lures within the Alexander Archipelago (inside waters) and the adjacent coastal region (outside waters). During the 135-d study in February, May, and September 1986–87, a total of 5,838 prerecruit chinook salmon were caught, of which 539 contained coded-wire tags with information on stock origin. Age -.0 chinook salmon were caught in September during their first year at sea; they originated predominately from stream-type stocks of southeastern Alaska. Age -.1 chinook salmon in February and May were primarily from stream-type stocks of southeastern Alaska; however, by September most were from ocean-type stocks from British Columbia, Washington, and Oregon streams. Most age -.2 chinook salmon were from ocean-type stocks of southern origin. Average net marine migration rates of different chinook salmon age groups ranged from 0.1 to 6.9 km/d; the highest rates were for age 1.0 fish from Washington and Oregon. For coded-wire-tagged chinook salmon of the same ocean age group, growth rates of ocean-type fish were significantly ($P<0.05$) higher than growth rates of stream-type fish during most periods. Spatial distribution also differed by race: stream-type fish predominated in inside waters and ocean-type fish in outside waters. This study identifies the importance of marine waters of southeastern Alaska as a nursery area for an amalgam of prerecruit chinook salmon stocks originating between Oregon and southeastern Alaska, a range of 1,800 km.

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Alaskan and non-Alaskan stocks of chinook salmon, *Oncorhynchus tshawytscha*, are harvested in southeastern Alaska waters predominately in hook-and-line marine fisheries; however, owing to a minimum size restriction of 71-cm total length, limited information exists on the temporal and spatial occurrence of smaller fish (prerecruits). Many North American stocks of chinook salmon embark on extensive marine migrations along the eastern Pacific Rim (Mason, 1965; Hartt and Dell, 1986). Some migrate across international or state boundaries and are intercepted in fisheries along migration corridors or in distant nursery areas. Consequently, many chinook salmon stocks have been overexploited, and rebuilding depressed runs is a major concern identified in the 1985 U.S.-Canada Pacific Salmon Treaty (Pacific Salmon Commission, 1986). A better understanding of the marine life history and distribution of chinook salmon populations will contribute to the development of management policies that are needed to restore the depressed stocks.

Not all chinook salmon migrate long distances. Some stocks in Oregon, Washington, British Columbia, and southeastern Alaska apparently do not migrate northward to any great extent (Mason, 1965; Nicholas and Hankin[1]), and many remain in inside waters all or much of their marine life (Hartt and Dell, 1986).

Two distinct races of chinook salmon have been identified: stream-type and ocean-type ("sea-type") (Gilbert, 1914; Healey, 1983). Stream-type fish are found throughout the geographic range of the species, whereas ocean-type fish occur primarily from British Columbia to California (Major et al., 1978; Healey, 1983). Stream-type chinook salmon remain in fresh water for one or more years before migrating to an estuary, whereas ocean-type chinook salmon migrate directly to an estuary as newly emerged fry or after 2–3 months of freshwater residence (Healey, 1983; Taylor, 1990). Prior to ocean entry, stream-type chinook salmon have a brief estuarine residence (Healey, 1983; Fisher and Pearcy, 1990) in contrast to ocean-type chinook salmon, which may reside in estuaries for up to three months (Healey, 1980; Myers and Horton, 1982; Nicholas and Hankin[1]; Reimers[2]).

[1] Nicholas, J. W., and D. J. Hankin. 1988. Chinook salmon populations in Oregon coastal river basins: description of life histories and assessment of recent trends in run strengths. Info. Rep. 88-1, Oregon Dep. Fish Wildl., Fish. Div., Res. and Develop. Section, Portland, OR 97207, 359 p.

[2] Reimers, P. E. 1973. The length of residence of juvenile fall chinook salmon in Sixes River, Oregon. Oregon Fish Comm. Res. Rep. 4(2), Oregon Dep. Fish Wildl., Portland OR 97201, 43 p.

In marine waters of southeastern Alaska, chinook salmon occur throughout the year (Cobb, 1910) and are harvested principally in a commercial troll fishery. Origins of stocks in this fishery are diverse, as documented by marine tagging studies, coded-wire tag (CWT) recoveries, and scale pattern analyses (Parker and Kirkness, 1956; Clark et al., 1985; Van Alen, 1988; Kissner[3]; Funk[4]). Throughout the history of this fishery, ocean-type chinook salmon of non-Alaskan origin have been the major harvest component (Parker and Kirkness, 1956; Van Alen and Wood, 1983; Olsen, 1992). Surprisingly, relatively little is known of the early marine distribution of prerecruit ocean-type fish after the initial summer at sea (Healey and Groot, 1987). In particular, it is not known whether prerecruit chinook salmon of different age groups within Alaskan marine waters are primarily of Alaskan or non-Alaskan origin.

Southeastern Alaska stocks of chinook salmon, which are primarily stream-type (Van Alen et al., 1986), migrate through inside marine waters of southeastern Alaska before their first marine winter (Orsi et al., 1987). In the summer and fall after their first marine winter, some portion of these stocks are recovered in southeastern Alaska waters (Hubartt and Kissner, 1987), whereas others migrate offshore to the North Pacific Ocean (Dahlberg et al.[5]). To identify the temporal and spatial distribution of prerecruit chinook salmon stocks in southeastern Alaska waters, we used commercial salmon trollers with small hooks and lures to sample prerecruits during February 1987 and May and September 1986 and 1987.

Methods

Sampling areas and times

Southeastern Alaska comprises the mainland coast and a large island group, the Alexander Archipelago, which covers about 100,000 km^2 (Fig. 1). Marine waters throughout this island group are a network of estuaries, fjords, and straits that lead into the Gulf of Alaska or Dixon Entrance. We sampled chinook salmon in "inside" and "outside" marine waters of the northern, central, and southern regions of the archipelago (Fig. 1). We defined "inside" waters as those within the Alexander Archipelago, typically adjacent to mainland southeastern Alaska, and "outside" waters as the coastal waters exposed to the Gulf of Alaska or Dixon Entrance near the outer coasts of Chichagof, Kuiu, and Prince of Wales Islands. Our selection criteria for sampling areas and times were influenced by the geographical localities of the major fishing ports in southeastern Alaska and by the availability of commercial trolling vessels during three off-season fishing periods separated by about four months.

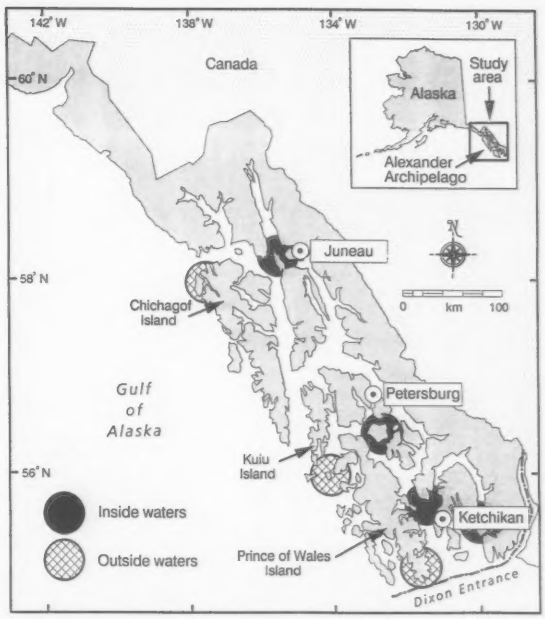

Figure 1

Inside and outside marine waters sampled in the northern, central, and southern regions of southeastern Alaska, 1986–87.

We sampled chinook salmon from 11.0–16.2-m chartered commercial power troll vessels during May and September 1986 and February, May, and September 1987 for a total of 1,156 h of fishing effort over a 135-d period (Table 1). The vessels were operated by experienced commercial salmon trollers, accompanied by fishery biologists. Inside and outside waters were typically sampled in each region and season; however, the central region was sampled only in September 1986, and inclement weather precluded sampling the outside waters of the southern region in February 1987 (Table 1).

[3] Kissner, P. D. 1977. A study of chinook salmon in Southeast Alaska. Alaska Dep. Fish Game, Sport Fish Div. Completion Rep., Vol. 18, Project F-9-8, Study AFS-41-5, Juneau, AK, 63 p.

[4] Funk, F. 1981. Analysis of southeastern Alaska troll fisheries data. Final Report, Contract 79-4, North Pacific Fishery Management Council Document 17. Alaska Dep. Fish and Game, Juneau, 103 p. + appendix.

[5] Dahlberg, M., S. Fowler, N. Maloney, and R. Heintz. 1991. Incidence of coded-wire tagged salmonids in commercial and research catches in the North Pacific Ocean and Bering Sea, 1990–1991. (INPFC [International North Pacific Fisheries Commission] Doc.), Auke Bay Laboratory, Alaska Fish. Sci. Cent., NMFS, NOAA, 11305 Glacier Hwy., Juneau, AK 99801-8626, 17 p.

Table 1

Hours of sampling effort for chinook salmon, *Oncorhynchus tshawytscha*, in inside and outside marine waters of southeastern Alaska over a 135-d period in February, May, and September 1986–87.

	February		May		September	
Region	Inside waters	Outside waters	Inside waters	Outside waters	Inside waters	Outside waters
1986						
Southern	—	—	—	—	79	40
Central	—	—	—	—	68	69
Northern	—	—	121	47	63	45
1987						
Southern	106	—	128	19	118	12
Northern	50	43	84	64	—	—
Total	156	43	333	130	328	166

Trolling gear

We fished with reduced-size replicates of commercial trolling gear. These small hooks and lures have proven more selective than standard commercial trolling gear in catching smaller sizes and younger age groups of chinook salmon (Orsi, 1987). The hooks were single Mustad no. 9510X3S, size 2/0, barbed, gap 1.6 cm, throat 2.0 cm. All lures used were 6.0-cm hootchies (plastic imitation squid) fished behind 9 × 28-cm flashers at 0.5–1.5 m/s and typically at 7.3-m depth intervals (7.3 m, 14.6 m, 21.9 m, 29.3 m, and 36.6 m). Five flasher and hootchie combinations were used concurrently on each of four trolling lines weighted with 13.6–22.7-kg lead "cannonballs." Areas where the bottom depth was shallower than 37 m were not sampled. Additional information on trolling methods or gear is given in Browning (1980) and Orsi et al. (1987).

To test whether the catch and size distribution of the youngest age group of chinook salmon in our study were representative of the population, we compared the catch and length of prerecruit chinook salmon caught on our standard small gear versus the catch and length of prerecruit salmon caught on smaller hooks (Mustad no. 9321, size 6, gap 0.7 cm, throat 1.0 cm) and hootchies (4.0 cm). We tested this for two days during September 1987 in inside waters of the southern region, where chinook salmon are known to occur during their first summer at sea. Equal numbers of each gear size and color were used on opposing vessel sides at equivalent depths; sides of the vessel were alternated each day. A chi-square (χ^2) test was used to test for significant differences ($P<0.05$) in catch between gear sizes, and a one-tailed t-test was used to test for significant differences ($P<0.05$) in the mean fork length of chinook salmon caught between gear sizes.

Fish processing

Chinook salmon were sampled while immobilized in an electric basket (Orsi and Short, 1987). While in the basket and lifted from the water, fish were identified, measured from tip of snout to fork of tail (to the nearest cm), tagged with a 6.4-cm-long Floy anchor tag (to ensure that fish had not already been caught), and sampled for scales from the preferred area (INPFC, 1957). All chinook salmon were released after tagging, except adipose-clipped fish under the Alaska minimum size limit (66 cm fork length [FL]=71 cm total length; Reed, 1972), which were retained to recover previously implanted CWT's (Jefferts et al., 1963). Sex and weight (to the nearest 0.1 kg) were recorded for all retained CWT chinook salmon.

Because field identification between chinook salmon and coho salmon, *O. kisutch*, in their first ocean year is sometimes difficult, salmon identifications during the charters in September were confirmed later by a scale reader. Identifications that did not correspond to the determinations of species by the scale reader were reexamined and reassigned as appropriate. Salmon with CWT's were also used to corroborate species identifications.

Scale, age, and sex analysis

Scales of chinook salmon were aged according to the methods of Van Alen and Wood (1983) and designated with the nomenclature of Koo (1962). The end of the calendar year was used as a break point for ocean-age assignment. For example, a 1984-brood-year chinook salmon that entered saltwater in 1986 was designated to be age 1.0 until 31 December 1986 and age 1.1 from 1 January to 31 December 1987.[6] Distinguishable ocean-winter annuli were present in scales taken from fish in February.

Data on age -.3 chinook salmon were not presented because few were caught; the hooks used in this study

[6] Numeral preceding the decimal point denotes the number of freshwater winters and the numeral following the decimal point denotes the number of marine winters. A dash before the decimal point indicates freshwater ages of 0 and 1.

tend to bend or straighten when large fish strike (Orsi, 1987). The data were also limited because we did not retain CWT fish >66 cm FL, which are typically age -.3 fish (Wright et al., 1972).

Scale and CWT ages, when available for the same fish, were used to compare age-determination techniques each season. Although freshwater and marine age can be misinterpreted from reported CWT release information, we assumed that the release year reported for CWT chinook salmon (Johnson and Longwill[7]) was also the year of seawater entry unless specified otherwise. We rejected age determinations based on scale analysis for fish in time periods or regions where they were unlikely to occur and were not substantiated by CWT recoveries; examples of this were age 0.0 fish in September in the northern and central regions, age -.0 fish in February and May and age 0.1 fish in February and May in the northern region.

We used χ^2 tests to examine differences in the proportion of male and female CWT chinook salmon by ocean-age group for each period. In September, all three ocean-age groups were present (i.e. age -.0, -.1, and -.2), whereas in February and May, data were available for only the age -.1 and -.2 ocean-age groups.

Length analysis

Box-and-whisker plots (Tukey, 1977) were performed for length ranges of each age group of chinook salmon within each region and time stratum to ensure accurate ageing and length representation. Values over 1.5 times the inner quartile range (IQR) were examined to identify extreme cases in length within a given age group that may have resulted from errors (by misinterpreting scale position on a scale card or by transposing age values). After extreme values had been examined and age or length reassigned as appropriate, box-and-whisker plots were reconstructed and values >3.0 times the IQR were eliminated from the database unless substantiated by CWT fish. The eliminated values constituted less than 0.5% of the data.

To demonstrate temporal and regional differences in length-frequency distributions of chinook salmon, length data were plotted for the three sequential sampling periods (September 1986, February 1987, and May 1987) from fish in inside and outside waters (when possible) in the northern and southern regions. All age groups were pooled in each length-frequency distribution.

To demonstrate seasonal size structure, fork lengths of ocean- and stream-type chinook salmon were plotted by age group and period. Fork-length data were pooled across regions, years, and waters.

Stock composition

Coded-wire tag recoveries from chinook salmon and the expanded number of fish represented by each tag code were used to determine stock composition. Expanded numbers represent the total number of fish represented by a CWT, based on the proportion of tagged fish in a release group. Origin of chinook salmon stocks represented by CWT's were pooled into three geographic groups: southeastern Alaska, British Columbia, and Washington or Oregon. Washington and Oregon stocks were combined because most recoveries from these regions originated from the Columbia River basin.

Catch per unit of effort (CPUE) was used with CWT recoveries to determine the spatial and temporal distribution of stock groups. To determine CPUE, expanded numbers for a particular age and stock group of chinook salmon were divided by the number of hours fished. This CPUE was computed separately for inside and outside waters and pooled across regions. For examining spatial distribution of individual age groups of ocean- and stream-type fish in inside and outside waters, CPUE was plotted against age for each stock group. For examining seasonal distribution, CPUE was plotted against ocean age and season for each stock group.

Migration and growth

Net migration rates for each CWT chinook salmon were calculated by dividing the hypothetical "straight line" marine distance traveled between release and recovery points by the number of days since release. Because of limited information on precise freshwater release sites for many CWT fish, freshwater distance was not included in the determination of migration distance. Direction of travel of each fish from its marine entrance point to its recovery locality was recorded to the nearest 45° directional interval (e.g. N=337.6°–22.5°, NE = 22.6°–67.5°, etc.).

Growth rates were compared between ocean- and stream-type CWT chinook salmon recovered during seven seasonal periods after release: age -.0 fish in September; age -.1 fish in February, May, and September; and age -.2 fish in February, May, and September. Specific growth rates, G, were determined for CWT chinook salmon by dividing the difference

[7] Johnson, J. K., and J. R. Longwill. 1988. Pacific salmonid coded wire tag releases through 1987. Regional Mark Processing Center, Pacific Marine Fisheries Commission, Metro Center, Suite 170, 2000 S.W. First Ave., Portland, OR 97201-5346, 228 p.

of the natural logarithms of the recovery weight and of the release weight by the change in time (Weatherley and Rogers, 1978). Because of limited samples of CWT fish, growth rates for ocean- or stream-type fish were pooled between years, regions, waters, and stock groups for each growth period. Ocean- and stream-type fish in each growth period were then tested for significant differences ($P<0.05$) in growth rates with t-tests.

Results

Gear selectivity

For the 2-d gear comparison conducted in inside waters of the southern Alaska region in September 1987, both sizes of hooks and lures caught similar numbers and mean fork lengths of age -.0 chinook salmon. In this comparison, 68 age -.0 chinook salmon were caught on our "standard" small gear and 59 on the smaller gear; numbers caught did not differ significantly ($\chi^2, P > 0.10$) by gear size. Mean fork length (27.6 cm) of age -.0 chinook salmon caught on "standard" small gear also did not differ significantly from mean fork length (27.0 cm) of fish caught on smaller gear (t-test, P=0.36). However, age -.0 chinook salmon caught on the "standard" small gear were larger (range, 22–37 cm FL) than those caught on the smaller gear (range, 15–34 cm FL).

Age, length, and sex composition

Of the 539 CWT chinook salmon sampled, 486 had scales that could be aged. Agreement between scale- and CWT-age was highest in September (95%) and lowest in February (79%); overall agreement was 90% (Table 2). The most common disagreement of age designations was the assignment of ocean-type chinook salmon (as determined by CWT's) as stream-type. Of the 51 disagreements in chinook salmon age determinations, 43 (84%) were ocean-type fish assigned stream-type designations; some of these disagreements may have been a result of fish that were released as ocean-type but that overwintered in freshwater, and therefore bore a "stream-type" scale pattern.

Age data for 5,838 chinook salmon were obtained from scales and CWT's in all sampling periods and regions in 1986–87 (Table 3). CWT's were represented in 36 of the 39 age-group–time-period strata. Age -.0 chinook salmon were caught only during September, and most were stream type (age 1.0); only a few ocean-type (age 0.0) chinook salmon were caught, all in the southern region. In February and May, age -.1 chinook salmon were primarily stream type (age 1.1); a few ocean-type fish (age 0.1) were caught only in the southern region. In September, however, both stream- and ocean-type age -.1 chinook salmon were caught in all regions. Age -.2 chinook salmon of the ensuing year were also a mixture of ocean- (age 0.2) and stream-type (age 1.2) fish in each season and region. Only four age -.3 CWT chinook salmon were recovered and all were ocean type (age 0.3).

Chinook salmon were larger and older in the northern than in the southern region in each sampling period (Fig. 2; Table 3). Length modes of chinook salmon within each region generally increased between September and May. The proportion of small fish (<30 cm FL) was highest in inside waters of both regions in September.

Mean length of chinook salmon increased with each successive period; and for each ocean-age group, stream-type fish were consistently longer than ocean-type fish for each period (Fig. 3). Differences in mean length of ocean- and stream-type chinook salmon

Table 2

Percent accuracy of scale reading (in parentheses) based on coded-wire–tag (CWT) age determinations of chinook salmon, *Oncorhynchus tshawytscha*, during February, May, and September 1986–87. n = number of fish.

CWT age	February		May		September		Total	
	n	(%)	n	(%)	n	(%)	n	(%)
0.0	—	—	—	—	1	(100)	1	(100)
0.1	1	(0)	7	(0)	48	(81)	56	(70)
0.2	19	(16)	23	(60)	9	(89)	51	(49)
1.0	—	—	—	—	152	(100)	152	(100)
1.1	64	(98)	90	(97)	31	(94)	185	(95)
1.2	3	(100)	36	(97)	2	(50)	41	(95)
Total	87	(79)	156	(87)	243	(95)	486	(90)

Table 3

Number of chinook salmon, *Oncorhynchus tshawytscha*, of different age groups (based on scale samples and coded-wire tags) caught in marine waters of the northern, central, and southern regions of southeastern Alaska during February, May, and September 1986–87. The number of coded-wire tags recovered is shown in parentheses.

Month and Region	Year	Age -.0		Age -.1		Age -.2		Total
		0.0	1.0	0.1	1.1	0.2	1.2	
February								
Northern	1987	—	—	—	20	62	86	168
		—	—	—	(0)	(4)	(1)	(5)
Southern	1987	—	—	8	520	62	50	640
				(1)	(69)	(17)	(3)	(90)
May								
Northern	1986	—	—	—	88	114	149	351
		—	—	—	(13)	(10)	(17)	(40)
Northern	1987	—	—	—	162	92	254	508
		—	—	—	(7)	(9)	(18)	(34)
Southern	1987	—	—	110	639	39	69	857
		—	—	(8)	(83)	(7)	(1)	(99)
September								
Northern	1986	—	38	318	114	30	17	517
		—	(0)	(19)	(7)	(2)	(1)	(29)
Central	1986	—	112	141	157	42	10	462
		—	(7)	(10)	(8)	(1)	(1)	(27)
Southern	1986	2	450	149	64	14	1	680
		(1)	(32)	(9)	(14)	(2)	(0)	(58)
Southern	1987	21	1,283	168	126	45	12	1,655
		(1)	(125)	(14)	(11)	(5)	(1)	(157)
Total		23	1,883	894	1,890	500	648	5,838
		(2)	(164)	(61)	(212)	(57)	(43)	(539)

were not as great among age -.2 fish as among younger fish, especially in September. Some age -.2 fish were probably not caught effectively then, owing to the small gear used; therefore the lengths of age -.2 chinook salmon in September did not extend far above one standard deviation from the mean (Fig. 3). Conversely, the lengths of age 0.0 chinook salmon caught in September, which did not extend far below one standard deviation from the mean, suggest that fish <15 cm FL were too small for our gear or were absent.

The overall sex ratio of the 539 CWT chinook salmon was nearly equal to 1.0, namely 275 males to 264 females. There were, however, significant differences in proportion of males by ocean-age group in September (χ^2, $P<0.01$) and May (χ^2, $P=0.05$) but not in February (χ^2, $P=0.75$). Percentage of males for each ocean age by season were as follows: September, age -.0 (57%), age -.1 (41%), and age -.2 (23%); May, age -.1 (56%) and age -.2 (40%); and February, age -.1 (56%) and age -.2 (52%). Of the CWT chinook salmon examined, most were immature; only a few age -.1 and -.2 males sampled in May were qualitatively assessed as maturing on the basis of coloration, shape, or enlarged gonads.

Origin and distribution

According to CWT recoveries, prerecruit chinook salmon in southeastern Alaska were from 74 stocks originating from Oregon to the northern region of southeastern Alaska, a range of 1,800 km (Table 4; Table 5).

Most stream-type chinook salmon of Alaska origin were caught in inside waters, whereas ocean-type fish of non-Alaska origin were slightly more abundant in outside than in inside waters (Fig. 4; Table 6). Most age -.0 stream-type chinook salmon from Alaska and British Columbia stocks were caught in inside waters, whereas those from Washington and Oregon stocks were caught in both inside and outside waters (Fig. 4; Table 6). Only two CWT age -.0 ocean-type chinook salmon were sampled; both were experimental hatchery releases from Alaska stocks caught in inside waters. Age -.1 and -.2 stream-type chinook salmon were mainly from Alaska stocks and were caught at a higher rate in inside waters than

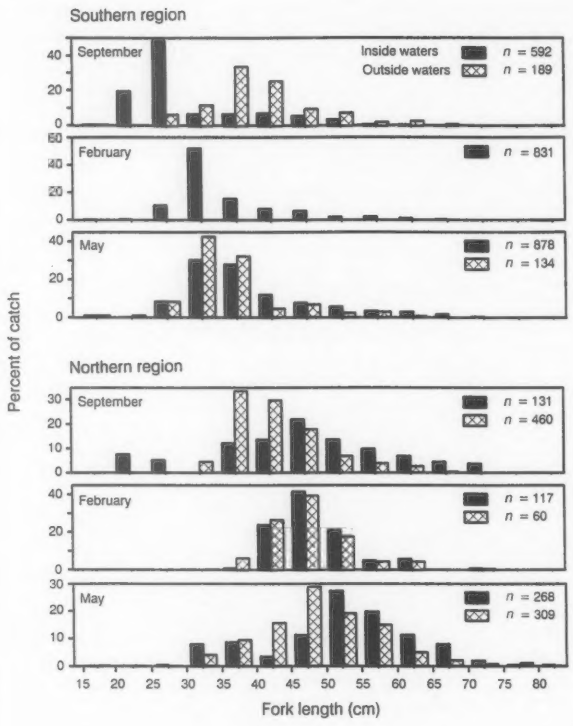

Figure 2

Length structure of chinook salmon, *Oncorhynchus tshawytscha*, sampled in inside and outside marine waters of the southern and northern regions of southeastern Alaska, September 1986 and February and May 1987.

Table 4

Major release localities of 539 coded-wire–tagged (CWT) chinook salmon, *Oncorhynchus tshawytscha*, recovered in marine waters of southeastern Alaska, February, May, and September 1986–87.

	CWT age at recovery						
Release locality	0.0	0.1	0.2	1.0	1.1	1.2	Total
Southeastern Alaska	2	4	—	127	204	40	377
Northern British Columbia	—	16	10	14	4	—	44
East coast Vancouver Island	—	12	14	—	—	—	26
West coast Vancouver Island	—	5	8	—	—	—	13
Fraser River drainage	—	2	—	—	—	—	2
Puget Sound	—	—	—	—	1	—	1
Strait of Juan de Fuca	—	—	1	—	—	—	1
Coastal Washington	—	8	12	—	—	—	20
Columbia River drainage	—	7	6	23	3	3	42
Coastal Oregon	—	7	6	—	—	—	13
Total	2	61	57	164	212	43	539

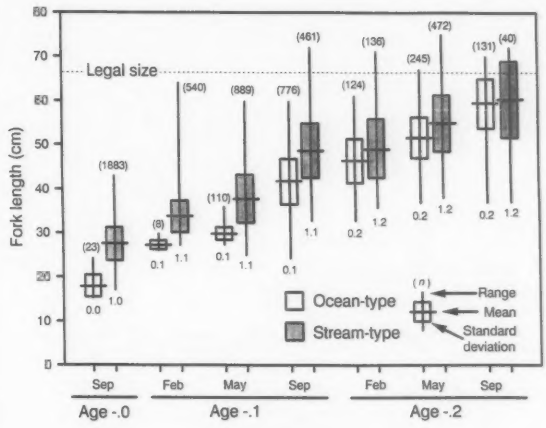

Figure 3

Length at age for ocean- and stream-type chinook salmon, *Oncorhynchus tshawytscha*, sampled in marine waters of southeastern Alaska during February 1987, May 1986–87, and September 1986–87. Sample sizes are in parentheses.

in outside waters; conversely, age -.1 and -.2 ocean-type fish were almost exclusively from British Columbia, Washington, or Oregon stocks and were caught at a slightly higher rate in outside waters (Fig. 4).

The CPUE of chinook salmon originating from each geographic region changed seasonally for each ocean-age group (Fig. 5). Age -.0 chinook salmon, which were caught only in September, were mainly of Alaska origin. All age -.1 chinook salmon in February were of Alaska origin except a few fish from British Columbia in inside waters (Fig. 5; Table 6). Among age -.1 fish caught in May, increasing numbers of fish from non-Alaska stocks were present; however, most of the fish were still of Alaska origin (Fig. 5). By September, an influx of age -.1 chinook salmon from British Columbia, Washington, or Oregon occurred, whereas the catches of age -.1 fish of Alaska origin diminished (Fig. 5). Most age -.2 chinook salmon were also from non-Alaska stocks for all periods.

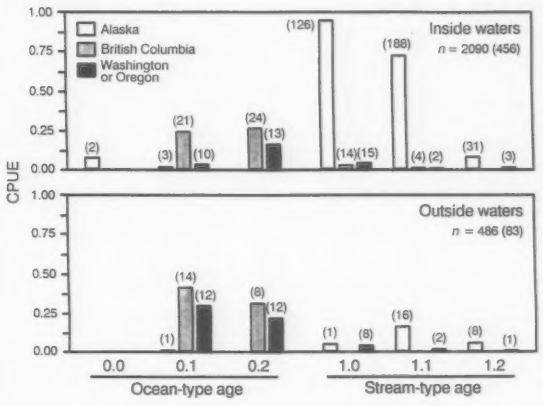

Figure 4

Catch rate by age and origin of ocean- and stream-type chinook salmon, *Oncorhynchus tshawytscha*, in inside and outside marine waters of southeastern Alaska, 1986–87. Catch rate is based on the expanded numbers of coded-wire–tagged fish caught per hour. Actual numbers of coded-wire–tagged fish are shown in parentheses.

Migration and growth

Assessment of migration direction and rates of the CWT chinook salmon was based on the origin and age of the stock group (Table 7). Stocks originating from British Columbia and Washington or Oregon generally traveled NW or N to reach our sampling localities, whereas stocks originating from within southeastern Alaska had no apparent directional tendency. Average net migration rates ranged from 0.1 to 6.9 km/d (Table 7). A decrease in average migration rates with increasing age occurred for all stock groups of ocean- and stream-type fish.

Table 5

Origin and age of 539 coded-wire–tagged chinook salmon, *Oncorhynchus tshawytscha*, recovered in marine waters of southeastern Alaska, February, May, and September 1986–87.

Origin		Number of chinook salmon					
		Age (yr)					
Locality	Latitude	0.0	0.1	0.2	1.0	1.1	1.2
Southeastern Alaska							
Speel Arm	58°04'N	—	—	—	—	3	3
Kasnyku Bay	57°13'N	—	—	—	—	2	3
Medvejie	57°01'N	—	—	—	—	4	1
Crystal Creek	56°53'N	—	—	—	—	—	2
Ohmer Creek	56°46'N	—	—	—	—	—	1
Osprey Lake	56°24'N	—	—	—	—	—	1
Little Port Walter	56°23'N	—	—	—	—	11	19
Earl West Cove	56°18'N	—	—	—	1	—	—
Unuk River	56°05'N	—	—	—	—	1	—
Chickamin River	55°47'N	—	—	—	2	4	—
Neets Bay	55°46'N	1	—	—	15	24	7
Carroll Inlet	55°39'N	1	1	—	63	67	—
Thomas Basin	55°21'N	—	3	—	—	—	—
Ketchikan Creek	55°21'N	—	—	—	6	23	—
Herring Cove	55°20'N	—	—	—	4	58	3
Whitman Lake	55°20'N	—	—	—	31	—	—
Tamgas Creek	55°01'N	—	—	—	5	7	—
Southeastern Alaska total		2	4	0	127	204	40
British Columbia							
Babine River	55°41'N	—	—	—	9	4	—
Upper Bulkley River	55°15'N	—	—	—	1	—	—
Hadenchild Creek	54°56'N	—	—	—	3	—	—
Cedar River	54°50'N	—	—	1	—	—	—
Copper River	54°32'N	—	—	2	—	—	—
Kitsumkalum River	54°31'N	—	3	—	—	—	—
Deep Creek	54°30'N	—	—	—	1	—	—
Hirsch Creek	54°05'N	—	4	—	—	—	—
Skeena River	54°01'N	—	2	2	—	—	—
Kitimat River	54°00'N	—	4	3	—	—	—
Kildala River	53°48'N	—	—	1	—	—	—
Snootli River	52°23'N	—	2	—	—	—	—
Atnarko River	52°22'N	—	1	—	—	—	—
Wannock River	51°40'N	—	—	1	—	—	—
Marble River	50°32'N	—	2	2	—	—	—
Tenderfoot Lake	50°25'N	—	1	—	—	—	-
Birkenhead River	50°19'N	—	1	—	—	—	—
Campbell Transit	50°02'N	—	—	2	—	—	—
Deepwater Bay	50°02'N	—	1	—	—	—	—
Quinsam River	50°02'N	—	6	8	—	—	—
Puntledge River	49°42'N	—	4	3	—	—	—
Big Qualicum	49°24'N	—	—	1	—	—	—
Little Qualicum	49°22'N	—	1	—	—	—	—
Robertson Creek	49°19'N	—	3	3	—	—	—
Thornton Creek	48°58'N	—	—	2	—	—	—
Nitinat River	48°40'N	—	—	1	—	—	—
British Columbia total		0	35	32	14	4	0
Washington or Oregon							
Kendall Creek	48°54'N	—	—	—	—	1	—
Elwha River	48°06'N	—	—	1	—	—	—
Soleduck River	48°03'N	—	3	2	—	—	—

Table 5 (continued)

Origin		Number of chinook salmon					
		Age (yr)					
Locality	Latitude	0.0	0.1	0.2	1.0	1.1	1.2
Washington or Oregon (continued)							
Wells Channel	47°55'N	—	—	—	2	—	—
Rocky Reach	47°32'N	—	—	—	5	—	—
Cook Creek	47°30'N	—	1	5	—	—	—
Fork Creek	46°33'N	—	—	2	—	—	—
Cowlitz River	46°31'N	—	—	1	—	—	—
N. Nemah River	46°30'N	—	1	1	—	—	—
Hanford	46°30'N	—	1	—	—	—	—
Naselle River	46°23'N	—	3	2	—	—	—
W. Fork Grays River	46°23'N	—	1	—	—	—	—
Columbia River	46°20'N	—	1	2	—	—	1
Lyons Ferry	46°15'N	—	—	—	4	—	—
N. Fork Lewis River	45°54'N	—	—	1	—	—	—
Wind River	45°51'N	—	—	—	1	—	—
Umitilla River	45°50'N	—	1	—	2	—	—
Spring Creek	45°42'N	—	—	1	—	—	—
Bonneville Dam	45°39'N	—	—	—	3	—	—
Washougal River	45°39'N	—	1	1	—	—	—
Tanner Creek	45°38'N	—	1	—	—	2	—
Trask River	45°25'N	—	1	2	—	—	—
Clackamas River	45°20'N	—	—	—	1	—	1
N. Santiam River	44°40'N	—	—	—	—	—	1
Yaquina Bay	44°37'N	—	2	—	—	—	—
Newport offshore	44°37'N	—	1	—	—	—	—
Deschutes River	44°36'N	—	—	—	2	—	—
McKenzie River	44°07'N	—	1	—	2	1	—
Willamette River	43°55'N	—	—	—	1	—	—
Coos Bay	43°20'N	—	—	2	—	—	—
Elk River	42°45'N	—	3	2	—	—	—
Washington or Oregon total		0	22	25	23	4	3

Growth rates were significantly higher (t-test, $P<0.05$) for ocean- than for stream-type CWT chinook salmon in four of the seven growth periods examined (Fig. 6). Sample sizes of certain age groups of fish in the three growth periods with no statistical significance were extremely limited (4 or less), although ocean-type chinook salmon in those cases also had higher growth rates than had stream-type fish. Mean growth rates generally declined as age increased and season progressed for ocean-type (2.35, 1.54, 1.20, 0.97, 0.71, 0.74, and 0.69% body wt/d) and stream-type (1.85, 0.99, 0.88, 0.78, 0.63, 0.64, and 0.58% body wt/d) chinook salmon (Fig. 6).

Discussion

This study has described the initial marine occurrence and distribution of ocean-type chinook salmon of non-Alaska origin in marine waters of southeastern Alaska. During earlier research on prerecruit chinook salmon in the central and northern regions of southeastern Alaska in May and September, Orsi et al. (1987) caught age 0.1 chinook salmon of non-Alaska origin in September, but not earlier. In our study, we caught age 0.1 non-Alaskan stocks of chinook salmon in the southern region in February, May, and September (Table 6). Consistent with Orsi et al. (1987), we also found an influx of non-Alaska age 0.1 chinook salmon by September in the central and northern regions (Table 6). We found age 0.2 chinook salmon of non-Alaska origin throughout marine waters of southeastern Alaska each season. Age 0.2 chinook salmon reach the minimum harvest size limit in the southeastern Alaska troll fishery in June and July (Olsen, 1992), and age 0.3 fish are the predominant harvest component (Van Alen and Olsen, 1986; Van Alen et al., 1986, 1987). Thus, non-

Table 6

Catch per hour of numbers represented by coded-wire–tagged (CWT) age groups of chinook salmon, *Oncorhynchus tshawytscha*, of southeastern Alaska (AK), British Columbia (BC), and Washington or Oregon (WO) origin recovered in inside and outside marine waters of the northern, central, and southern regions of southeastern Alaska in February, May, and September 1986–87. The actual number of CWT's is shown in parentheses.

	Inside waters						Outside waters					
Region	0.0	1.0	0.1	1.1	0.2	1.2	0.0	1.0	0.1	1.1	0.2	1.2
Southeastern Alaska origin												
February												
Northern	—	—	—	—	—	—	—	—	—	—	—	—
Southern	—	—	—	2.46	—	0.08	—	—	—	—	—	—
	—	—	—	(67)	—	(3)	—	—	—	—	—	—
May												
Northern	—	—	—	0.06	—	0.20	—	—	—	0.08	—	0.15
	—	—	—	(12)	—	(24)	—	—	—	(7)	—	(8)
Southern	—	—	0.03	1.96	—	0.01	—	—	0.09	0.98	—	—
	—	—	(2)	(78)	—	(1)	—	—	(1)	(2)	—	—
September												
Northern	—	—	—	0.08	—	0.09	—	—	—	0.35	—	—
	—	—	—	(2)	—	(1)	—	—	—	(4)	—	—
Central	—	0.87	—	0.43	—	0.05	—	—	—	—	—	—
	—	(4)	—	(8)	—	(1)	—	—	—	—	—	—
Southern	0.29	3.60	0.02	0.16	—	0.01	—	0.28	—	0.14	—	—
	(2)	(122)	(1)	(21)	—	(1)	—	(1)	—	(3)	—	—
AK total	(2)	(126)	(3)	(188)	—	(31)	—	(1)	(1)	(16)	—	(8)
British Columbia origin												
February												
Northern	—	—	—	—	0.87	—	—	—	—	—	0.57	—
	—	—	—	—	(2)	—	—	—	—	—	(2)	—
Southern	—	—	0.01	0.02	0.75	—	—	—	—	—	—	—
	—	—	(1)	(2)	(15)	—	—	—	—	—	—	—
May												
Northern	—	—	—	—	0.03	—	—	—	—	—	0.65	—
	—	—	—	—	(3)	—	—	—	—	—	(6)	—
Southern	—	—	0.25	0.02	0.52	—	—	—	—	—	—	—
	—	—	(4)	(2)	(3)	—	—	—	—	—	—	—
September												
Northern	—	—	0.89	—	—	—	—	—	1.87	—	—	—
	—	—	(3)	—	—	—	—	—	(6)	—	—	—
Central	—	—	0.36	—	—	—	—	—	0.59	—	—	—
	—	—	(1)	—	—	—	—	—	(6)	—	—	—
Southern	—	0.08	0.45	—	0.07	—	—	—	0.11	—	—	—
	—	(14)	(12)	—	(1)	—	—	—	(2)	—	—	—
BC total	—	(14)	(21)	(4)	(24)	—	—	—	(14)	—	(8)	—
Washington or Oregon origin												
February												
Northern	—	—	—	—	—	0.02	—	—	—	—	—	—
	—	—	—	—	—	(1)	—	—	—	—	—	—
Southern	—	—	—	—	0.02	—	—	—	—	—	—	—
	—	—	—	—	(2)	—	—	—	—	—	—	—
May												
Northern	—	—	—	—	0.04	0.02	—	—	—	0.02	0.47	0.01
	—	—	—	—	(1)	(2)	—	—	—	(1)	(9)	(1)
Southern	—	—	0.01	0.01	0.15	—	—	—	—	—	0.05	—
	—	—	(1)	(1)	(3)	—	—	—	—	—	(1)	—
September												
Northern	—	—	—	—	0.19	—	—	—	1.56	0.05	0.09	—
	—	—	—	—	(1)	—	—	—	(10)	(1)	(1)	—

Table 6 (continued)

Region	Inside waters 0.0	1.0	0.1	1.1	0.2	1.2	Outside waters 0.0	1.0	0.1	1.1	0.2	1.2
Washington or Oregon origin (continued)												
Central	—	—	0.07	—	0.18	—	—	0.07	—	—	—	—
	—	—	(3)	—	(1)	—	—	(3)	—	—	—	—
Southern	—	0.15	0.08	0.01	0.37	—	—	0.14	0.11	—	0.18	—
	—	(15)	(6)	(1)	(5)	—	—	(5)	(2)	—	(1)	—
WO total	—	(15)	(10)	(2)	(13)	(3)	—	(8)	(12)	(2)	(12)	(1)
Total	(2)	(155)	(34)	(194)	(37)	(34)	—	(9)	(27)	(18)	(20)	(9)

Alaska ocean-type chinook salmon of age 0.1 begin to arrive in the marine waters of southern region of southeastern Alaska in February and May, and by September, non-Alaska chinook salmon age 0.1, as well as those 0.2 and 0.3, are distributed throughout the marine waters of southeastern Alaska.

The temporal and spatial distribution of stream-type chinook salmon in southeastern Alaska appears more complex than that of ocean-type stocks. We found that age 1.0 chinook salmon in September originated from southeastern Alaska, British Columbia, Washington, and Oregon. Age 1.0 stocks from southeastern Alaska were almost exclusively found in inside waters of the southern and central regions; Orsi et al. (1987) also identified age 1.0 fish from these stocks in the northern region. Age 1.0 stocks from British Columbia were found exclusively in inside waters of the southern region. Age 1.0 chinook salmon from Washington and Oregon stocks were recovered in both inside and outside waters of the southern region and in outside waters of the central region. These recoveries corroborate the external tagging studies of Hartt and Dell (1986). Healey (1983, 1991) reported that the residence of stream-type chinook salmon in estuaries and sheltered coastal waters is generally brief and that fish move offshore during their first summer at sea, in contrast to ocean-type fish, which remain in sheltered coastal waters. Our data support his hypothesis with respect to stream-type chinook salmon from Washington and Oregon. However, our recoveries of Alaska and British Columbia stream-type chinook salmon in inside waters during September, and during the ensuing year in February and May, suggest a more protracted residence or limited marine migration for portions of stocks from these regions.

The limited marine migration of some Alaska stream-type stocks of chinook salmon could have a genetic basis. Although Alaska stocks of chinook salmon are almost exclusively stream-type, electrophoretic evidence suggests that southeastern Alaska stocks are genetically intermediate between stream-type stocks of western Alaska and ocean- and stream-type stocks of the Pacific Northwest (Gharrett et al., 1987). Therefore, following the Wisconsinan glacial age, some southeastern Alaska drainages were probably colonized by ocean-type stocks. These fish may have selected a stream-type freshwater life history trait as a result of low "growth opportunity" in northern lati-

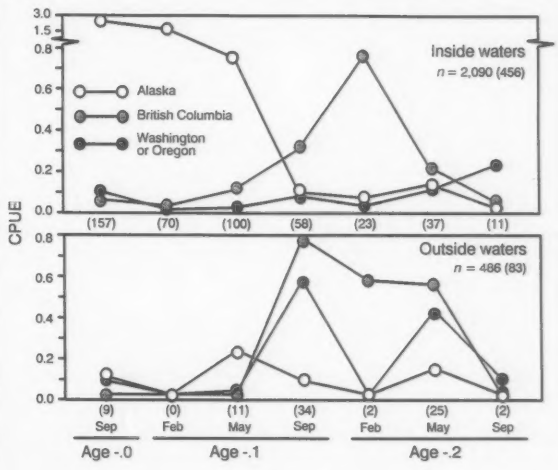

Figure 5

Catch rate of chinook salmon, *Oncorhynchus tshawytscha*, by ocean age and season in inside and outside marine waters of southeastern Alaska, 1986–87. Catch rate is based on the expanded numbers of coded-wire–tagged fish caught per hour. Actual numbers of coded-wire–tagged fish are shown in parentheses.

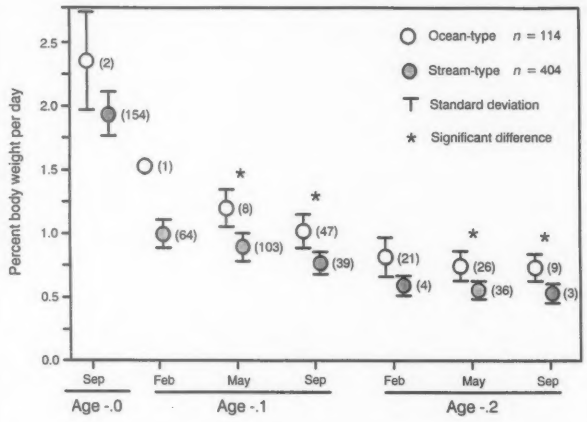

Figure 6

Growth rates of ocean- and stream-type chinook salmon, *Oncorhynchus tshawytscha*, by ocean age and season in marine waters of southeastern Alaska, 1986–87. Mean growth rates are based on coded-wire–tag recoveries shown in parentheses. Significant differences ($P<0.05$) in growth rates between ocean- and stream-type chinook salmon were denoted by an asterisk.

Table 7

Migration rate and direction of coded-wire–tagged ocean- and stream-type chinook salmon, *Oncorhynchus tshawytscha*, recovered in inside and outside marine waters of the northern, central, and southern regions of southeastern Alaska in February, May, and September 1986–87. Stock group designations: AK = Southeastern Alaska, BC = British Columbia, and WO = Washington or Oregon. *n* = number of fish.

Stock group	Age	*n*	Average migration			Migration direction							
			km	Days out	Rate km/d	N	NE	E	SE	S	SW	W	NW
Ocean-type													
AK	0.0	2	41	95	0.4	—	—	—	—	1	1	—	—
AK	0.1	4	37	345	0.1	—	—	1	1	—	1	1	—
AK	0.2	—	—	—	—	—	—	—	—	—	—	—	—
BC	0.0	—	—	—	—	—	—	—	—	—	—	—	—
BC	0.1	35	653	446	1.5	—	—	—	—	—	—	2	33
BC	0.2	32	741	642	1.2	—	—	—	—	—	—	—	32
WO	0.0	—	—	—	—	—	—	—	—	—	—	—	—
WO	0.1	22	1,430	397	3.6	6	—	—	—	—	—	—	16
WO	0.2	25	1,325	686	1.9	—	—	—	—	—	—	—	25
Stream-type													
AK	1.0	127	39	120	0.3	3	1	15	17	38	14	24	15
AK	1.1	204	64	354	0.2	9	4	19	37	70	15	17	33
AK	1.2	40	176	734	0.2	19	0	1	1	1	2	3	13
BC	1.0	14	183	197	0.9	—	—	—	—	—	—	—	14
BC	1.1	4	175	349	0.5	—	—	—	—	—	—	1	3
BC	1.2	—	—	—	—	—	—	—	—	—	—	—	—
WO	1.0	23	1,153	168	6.9	10	—	—	—	—	—	—	13
WO	1.1	4	1,354	486	2.8	—	—	—	—	—	—	—	4
WO	1.2	3	1,546	729	2.1	—	—	—	—	—	—	—	3

tudes owing to temperature and photoperiod regimes (Taylor, 1990) but retained the early ocean-distribution pattern characteristic of their ocean-type lineage.

Differences in length and spatial occurrence of prerecruit ocean- and stream-type chinook salmon in our study were similar to those found later in the commercial troll fishery of southeastern Alaska. Our stream-type chinook salmon were larger and more prevalent in inside waters than were ocean-type chinook salmon of the same ocean-age group. In the southeastern Alaska troll fishery, stream-type chinook salmon are also larger than ocean-type chinook salmon of the same ocean-age group (Van Alen and Wood, 1983; Van Alen et al., 1987), and ocean-type chinook salmon are generally more prevalent than stream-type chinook salmon in outside waters (Van Alen and Olsen, 1986; Van Alen et al., 1987).

Prerecruit chinook salmon were older and larger in the northern regions. Age data from the commercial troll fishery of southeastern Alaska similarly reveal that chinook salmon are older in northern regions (Van Alen and Olsen, 1986; Van Alen et al., 1987). In British Columbia, Healey (1986) found that age 0.2 and age 0.3 troll-caught chinook salmon dominated the catch, that larger age 0.3 fish were more common in northern and central regions, and that smaller age 0.2 fish were more common farther south off Vancouver Island. Age 0.2 chinook salmon also dominate the catch in the Strait of Georgia (Argue et al., 1977; Carter et al., 1986) and off the Washington coast (Wright et al., 1972). However, increased harvest of age 0.2 fish southward is also a reflection of lower minimum-size limits in these fisheries.

The 15–43 cm FL range of our troll-caught age -.0 chinook salmon during September in Alaska is consistent with other studies. Hartt and Dell (1986) reported a 16–36 cm FL range for age -.0 chinook salmon caught with small-mesh purse seines fished in the northeastern Gulf of Alaska from July to October. In another seine study, Fisher and Pearcy (1995) reported a 9–32 cm FL range for age -.0 chinook in shelf waters off the Oregon and Washington coasts from May to September. Of the smaller chinook salmon captured, Fisher and Pearcy (1995) found that chinook salmon <15 cm FL were most abundant in July and August and that chinook salmon <13 cm FL (primarily age 0.0 fish) were closely associated with the warm, low-salinity waters of the Columbia River plume. Moreover, Miller et al. (1983) hypothesized that offshore movement of chinook salmon is size dependent because few chinook salmon <13 cm FL are found in waters >30 m. Our gear test with smaller hooks and lures did indicate a lower length range for age -.0 fish sampled, but fish <15 cm FL were not encountered. Therefore, the absence of fish <15 cm FL in our study may have been a function of the deeper water (>37 m) that we sampled or of our later sampling time (September) when small age -.0 fish were unavailable. In contrast to the seine sampling, the greater upper length range for this age group caught on troll gear may be attributed to seine avoidance by larger chinook salmon. Chinook salmon occur deeper as they increase in length (Orsi and Wertheimer, 1995). Consequently, troll sampling may provide a more representative sample of larger age -.0 chinook salmon within this age group if larger fish were deeper than the seine nets.

Fishery size limits and gear selectivity can influence length distributions. The 66-cm-FL Alaska size limit for chinook salmon had little effect on the length distribution of the age -.0 or -.1 chinook salmon sampled in our study, because the range of length for these age groups seldom exceeded the size limit. However, the range of length for age -.2 chinook salmon usually exceeded the size limit. In the southeastern Alaska troll fishery, Van Alen and Wood (1983) have shown that the percent contribution of age -.2 chinook salmon increases during summer. Therefore, many larger age -.2 chinook salmon may have been removed by the troll fishery before we sampled in September. Healey (1986) reported that the average length of age 0.2 chinook salmon in the British Columbia troll fishery remained relatively constant over the fishing season and attributed this constancy to new recruits growing to legal size. Selectivity by trolling gear also influences length distribution; Orsi (1987) reported significantly more age-.2 chinook salmon caught in September–October on standard commercial gear than on small trolling gear. Other studies also document that large chinook salmon are generally caught with large trolling gear, such as plugs (e.g. Milne, 1955; Boydstun, 1972; Orsi et al., 1993). Thus, fishery size limits and removals, as well as gear selectivity, affected the length structure of age -.2 chinook salmon in our study.

Mean fork length of stream-type chinook salmon was consistently greater than that of ocean-type fish of the same ocean-age group, but this difference was less pronounced as ocean age increased. The greater mean fork length of age -.0 stream-type fish is a function of greater freshwater age and an earlier time of ocean entry. However, mean fork length of age -.2 ocean- and stream-type fish were nearly equivalent in September. Although Healey (1991) reported that rates of growth were similar between ocean- and stream-type fish during their ocean life, we found significantly higher growth rates for ocean-type fish. The higher growth rates for ocean-type fish in our study may explain why mean fork length of ocean- and stream-type fish converged as ocean age increased.

Average net migration rates decreased with increasing age for all stock groups of ocean- and stream-type chinook salmon. This decreased migration rate for older fish may be a consequence of residency in the sampling area or of interception of fish during a circuitous return migration. Highest migration rates were for age 1.0 fish from Washington and Oregon (6.9 km/d). Fisher and Pearcy (1995) reported that age 1.0 chinook salmon (75 km up the Columbia River) migrated at an average net rate of 4.1 km/d to ocean capture locations off Washington and Oregon. Our higher average net migration rates for age 1.0 chinook salmon from Washington and Oregon may have been a function of our capture locality, which would favor recoveries of fish from these stocks that had migrated northward most rapidly.

This study identifies the marine waters of southeastern Alaska as an important nursery area for an amalgam of prerecruit chinook salmon stocks originating from Oregon to Alaska. Stream-type stocks from southeastern Alaska and northern British Columbia typically use inside waters during their first year at sea; at the same time stream-type stocks of Washington and Oregon use both inside and outside waters. Ocean-type stocks from British Columbia, Washington, and Oregon first appear in marine waters of southeastern Alaska after their first winter at sea and use waters throughout the region during their second and third years at sea. Although our study on prerecruit chinook salmon has contributed to our understanding of the temporal and spatial occurrence of this species in southeastern Alaska, additional studies of prerecruits in this region are needed to further identify migration routes, distribution patterns, and residency time of specific stock groups.

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Estimating the mean and variance from highly skewed marine data

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Abstract.—The spatial distribution of marine organisms is highly patchy. Because of this patchy distribution, data from marine abundance surveys are highly skewed and have a large variance. Compounding the problem of estimating the mean abundance from such data, is that occasionally a relatively huge catch will occur. These large catches are not "outliers" but do dominate the estimates of the mean and variance. A lognormal model of the nonzero survey values (a Δ-distribution) is used to model survey data. The estimators, based on the lognormal model, appear to be much more efficient for marine data than the usual sample estimators. In particular, the lognormal-based estimators provide reasonable estimates for data sets that contain a very large catch. The properties and efficiency of the Δ-distribution estimators are examined and the techniques are applied to various marine data sets.

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Characteristically, the observed distribution of abundance data generated by marine surveys has a large variance, is highly skewed to the right, and contains a substantial proportion of zeros. Because of this large variability, the sample mean has a low level of precision even for relatively intensive surveys (Grosslein, 1971; Godø, 1994; Pennington and Godø, 1995). A common problem in the analyses and interpretation of skewed survey data, is that a single immense catch may account for 50% or more of the total catch during a survey (Sissenwine, 1978; Dew, 1990; McConnaughey and Conquest, 1992; Bowering and Brodie, 1994). These extreme values not only greatly affect the estimate of the mean but also of the variance (Otto, 1986). As McConnaughey and Conquest (1992) observed, although these large values cause much uncertainty for management, they reflect the spatial distribution of the species and are not outliers that should be discarded. In practice, the use of more efficient sampling schemes or estimators is the only realistic way to increase survey precision; the total number of samples that can be taken is limited by the high cost of sampling at sea (Gunderson, 1993).

One possible way to increase the precision of survey estimates is to model the observed distribution of catches and exploit the model's properties to develop more efficient estimators of population parameters (see, e.g. Pennington, 1983; MacLennan and MacKenzie, 1988; Lo et al., 1992; McConnaughey and Conquest, 1992; Conquest et al., 1996; Stefánsson, in press). For marine data, the distribution of the nonzero values is often well approximated by a lognormal distribution (e.g. Pennington, 1983; Smith, 1988; McConnaughey and Conquest, 1992; Conquest et al., 1996). Myers and Pepin (1990) found that of the 69 marine data sets they examined, only 5 differed significantly from the lognormal distribution. Thus the lognormal model has been used as a basis for developing survey abundance estimators (e.g. Pennington, 1983, 1986; Lo et al., 1992; McConnaughey and Conquest, 1992) and for estimating commercial catch (Conquest et al., 1996).

It is not surprising that marine abundance data often appear to follow a lognormal distribution. The factors that determine abundance over a region seem to have a multiplicative effect. When this is the case, survey data will be approximately lognormally distributed by the central limit theorem (see, e.g. Aitchison and Brown, 1957). More generally, the lognormal model has been useful for analyzing a wide range of ecological data. As Dennis and Patil (1988) put it: "Ecological abundance data are intrinsically positive, with a few enormously high data points typically arising in every study. The lognormal distribution is an ideal descriptor of such

data with a positive range, right skewness, heavy tail, and easily computed parameter estimates."

To estimate efficiently the mean of skewed marine survey data and to be able to assess its precision, I examined an estimator based on a lognormal model of the distribution. I present the estimator's theoretical efficiency, assess its performance by applying it to several real marine data sets, and give methods for constructing confidence intervals.

Statistical methods

Suppose the nonzero catches generated by a survey are lognormally distributed, i.e. the logged values are normally distributed. If the distribution contains a proportion of zeros, then it is called a Δ-distribution (Aitchison and Brown, 1957). If zeros do not occur, then it is the usual lognormal distribution.

Estimating the mean and variance of the Δ-distribution

As is the case for any distribution, the sample average, $\bar{x}$, and variance, s_x^2, are unbiased estimators of the mean and variance of the Δ-distribution. Because of the properties of the lognormal distribution, the minimum variance unbiased estimators (denoted by c and d) of the mean and variance of the Δ-distribution are given by (Aitchison and Brown, 1957)

$$c = \begin{cases} \frac{m}{n}\exp(\bar{y})g_m(s^2/2), & m>1 \\ \frac{x_1}{n}, & m=1 \\ 0, & m=0 \end{cases} \quad (1)$$

and

$$d = \begin{cases} \frac{m}{n}\exp(2\bar{y})\left\{g_m(2s^2)-\left(\frac{m-1}{n-1}\right)g_m\left(\frac{m-2}{m-1}s^2\right)\right\}, & m>1 \\ \frac{x_1^2}{n}, & m=1 \\ 0, & m=0 \end{cases} \quad (2)$$

where n is the number of observations, m is the number of nonzero values, $y = \ln(x)$, $\bar{y}$, and s^2 are the sample mean and variance of the logged nonzero values, x_1 denotes the single untransformed value when m equals one, and $g_m(t)$, which is a function of m and t (e.g. $t = s^2/2$ in Equation 1), is defined by

$$g_m(t) = 1+\frac{m-1}{m}t + \sum_{j=2}^{\infty}\frac{(m-1)^{2j-1}}{m^j(m+1)(m+3)\ldots(m+2j-3)}\times\frac{t^j}{j!}. \quad (3)$$

Estimating the variance of $\bar{x}$ and c

Again for the Δ-distribution, the sample mean, $\bar{x}$, and c are both unbiased estimators of the mean. Likewise, the sample variance, s_x^2, and d are unbiased estimators of the population variance. If $\bar{x}$ is used to estimate the mean, then s_x^2/n, the sample variance divided by the sample size, is an estimate of the variance of $\bar{x}$. But s_x^2 can be a very inefficient estimator compared with d, and, therefore, it is frequently recommended that d/n be used to estimate the variance of $\bar{x}$ (Aitchison and Brown, 1957). The minimum variance unbiased estimator of the variance of c is given by (Pennington, 1983)

$$\mathrm{var}_{est}(c) = \begin{cases} \frac{m}{n}\exp(2\bar{y})\left\{\frac{m}{n}g_m^2(s^2/2)-\left(\frac{m-1}{n-1}\right)g_m\left(\frac{m-2}{m-1}s^2\right)\right\}, & m>1 \\ \left(\frac{x_1}{n}\right)^2, & m=1 \\ 0, & m=0 \end{cases} \quad (4)$$

If $m = n$, i.e. there are no zeros, then Equations 1, 2, and 4 reduce to the usual estimators for the lognormal distribution.

Relative efficiency of $\bar{x}$ and c

For the two estimators of the mean, $\bar{x}$ and c, the one with the smallest variance is the most efficient estimator. The formulas in the last section give estimates of the variance based on the particular sample drawn from the distribution. The expected or true variance of $\bar{x}$ is (Aitchison and Brown, 1957)

$$\mathrm{var}(\bar{x}) = \frac{\exp(2\mu+\sigma^2)}{n}\left\{p[\exp(\sigma^2)-1]+p(1-p)\right\}, \quad (5)$$

where μ is the mean and σ is the standard deviation of the log-transformed nonzero values, and p is the proportion of nonzeros. Smith (1988) derived the expected value of $var_{est}(c)$, which, in the same notation as above, is given by

$$\mathrm{var}(c) = \frac{\exp(2\mu+\sigma^2)}{n} \times \left\{\frac{1}{n} E_{m>0}\left[m^2\left\{\exp(\sigma^2/m) g_m(\sigma^4/2m) - 1\right\}\right] + p(1-p)\right\}, \quad (6)$$

where

$$E_{m>0}[\cdot] = \sum_{m=1}^{n} m^2 \binom{n}{m} p^m (1-p)^{n-m} \times \left\{\exp(\sigma^2/m) g_m(\sigma^4/2m) - 1\right\}.$$

It can be shown using results from Bradu and Mundlak (1970) that the $var(c)$ is always less than or equal to $var(\bar{x})$, both decrease as n increases, but $var(c)$ decreases more quickly than does $var(\bar{x})$. For values of σ^2 typical for marine data, $var(c)$ is considerably smaller than $var(\bar{x})$ (Pennington, 1986; Smith, 1988). This can be seen in Figure 1 which contains plots of $var(c)$ divided by $var(\bar{x})$ versus sample size for a range of σ^2's appropriate for marine survey data.

Tracking trends in abundance

For a series of marine surveys, it is usually assumed that the mean catch per tow is proportional to population size. If this is the case, then the estimator, c, is an index of abundance. The mean of the lognormal distribution is given by $\exp(\mu + \sigma^2/2)$. McConnaughey and Conquest (1992) have suggested that for lognormally distributed survey data, $\exp(\bar{y})$, a slightly biased estimate of $\exp(\mu)$, may be a more stable index for following trends in abundance than estimates of the mean. That is, if σ^2 is constant over time (which is equivalent to the coefficient of variation of the untransformed variable being constant) then $\exp(\mu)$, the median of the lognormal distribution, will also be proportional to abundance. The variance of $\exp(\bar{y})$ can be considerably smaller than the variance of c.

The mean of the Δ-distribution is $p[\exp(\mu + \sigma^2/2)]$. If the mean is proportional to population size and σ^2 is constant for a survey series, then $p[\exp(\mu)]$ will also be an index of abundance. It can be shown with techniques similar to those in Pennington (1983) that the minimum variance unbiased estimator, k, of $p[\exp(\mu)]$ is

$$k = \begin{cases} \frac{m}{n}\exp(\bar{y}) g_m\left(\frac{-s^2}{2(m-1)}\right), & m > 1 \\ \frac{x_1}{n}, & m = 1 \\ 0, & m = 0 \end{cases} \quad (7)$$

and the minimum variance unbiased estimator of the variance of k is given by

$$\mathrm{var}_{est}(k) = \begin{cases} \frac{m}{n}\exp(2\bar{y})\left\{\frac{m}{n} g_m^2\left(\frac{-s^2}{2(m-1)}\right) - \left(\frac{m-1}{n-1}\right) g_m\left(\frac{-2s^2}{m-1}\right)\right\}, & m > 1 \\ \left(\frac{x_1}{n}\right)^2, & m = 1 \\ 0, & m = 0 \end{cases} \quad (8)$$

As before, if $m = n$, then Equations 7 and 8 reduce to the lognormal case (Bradu and Mundlak, 1970).

Confidence intervals

If n is large, then $c \pm 2[var_{est}(c)]^{1/2}$ and $k \pm 2[var_{est}(k)]^{1/2}$ are approximately 95% confidence intervals. For smaller n, a conservative approach for constructing confidence intervals is to calculate separate in-

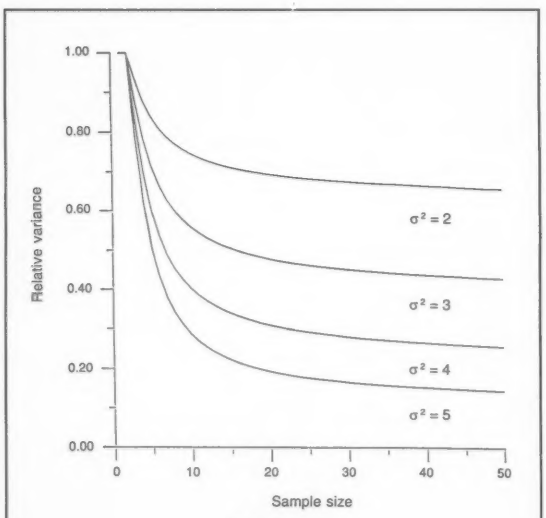

Figure 1

The relative efficiency of the estimators c and $\bar{x}$ for estimating the mean of the Δ-distribution. The plots show the $var(c)$ divided by the $var(\bar{x})$ as a function of sample size when the variance of the nonzero logged values, σ^2, equals 2, 3, 4, and 5, and when the proportion of nonzero values, p, is 0.8.

tervals for p and for the mean (or median) of the lognormally distributed nonzero values. For example, if (p_L , p_U) is a 95% confidence interval for p and (L, U) is a 95% interval for the mean (or median) of the lognormal component (see, e.g. McConnaughey and Conquest, 1992), then (p_LL, p_UU) will have a confidence level of at least 90% (=0.95 × 0.95).

Examples

There are two types of data sets that are typical for marine abundance surveys. The first type has a single large catch that can be many times larger than the next biggest catch. This huge catch may account for more than 50% of the total catch taken during the survey. The other category, and the more common type, is that the distribution of catches is highly skewed, as is the case for the first type, but there are no isolated large catches that dominate the total catch. These are the basic types of data sets that would be expected if samples are taken from a highly skewed lognormal distribution.

Isolated large catches

Occasionally, a very large value can occur when samples are drawn from a lognormal distribution. The first example (Table 1) is an artificial data set generated from a lognormal distribution with $\mu = 0$ and $\sigma^2 = 4$. The mean of the distribution is 7.4 and its variance is 2,926. Because of one large point in the sample, the estimates, $\bar{x} = 38.8$ and $s_x^2 = 63{,}320$, are much larger than the true values. The estimated standard error of the sample mean based on the sample variance is 35.6 [= $(63{,}320/50)^{1/2}$].

The sample estimates of the logged values are $\bar{y} = 0.175$ and $s^2 = 3.921$. Hence the estimates of the mean and variance from the minimum variance unbiased estimators are [Equations 1 and 2, $m = n = 50$]

$$c = \exp(0.175)g_{50}(1.961) = 7.6$$

and

$$d = \exp(0.350)\left\{g_{50}(7.842) - g_{50}\left(\frac{48}{49}\times 3.921\right)\right\}$$
$$= 1.42\times(922.83 - 34.07) = 1261,$$

which are much closer to the true values than are the ordinary sample estimates. The estimate of the standard error of the sample mean using d is 5.0 [=$(1261/50)^{1/2}$] as compared with an estimate of 35.6 based on the sample variance. The expected standard error of the sample mean (when $n = 50$) is 7.6 [=$(2926/50)^{1/2}$].

The estimated variance of c is given by (Equation 4)

Table 1

An artificial data set generated from a lognormal distribution, catch per unit of effort (CPUE) data for red king crab from a 1991 trawl survey in the Bering Sea, and CPUE data for petrale sole from a 1992 survey off the west coast of the United States.

Artificial data									
0.03	0.03	0.04	0.09	0.14	0.18	0.20	0.22	0.25	0.25
0.25	0.27	0.27	0.27	0.30	0.38	0.40	0.42	0.51	0.55
0.61	0.74	0.80	0.82	0.84	0.86	1.02	1.41	1.91	2.08
2.35	2.72	3.20	3.21	3.22	3.26	3.39	4.21	4.76	5.61
7.47	8.06	8.25	8.80	8.85	9.10	12.92	16.94	23.61	1782.19
Red king crab CPUE[1]									
65	66	69	71	72	73	76	78	78	79
81	83	84	85	86	108	141	144	152	154
154	157	160	161	165	183	204	234	263	265
292	313	317	339	413	435	455	469	569	609
625	746	758	813	909	1056	1145	1197	1339	1789
1842	2520	4194	4286	5424	32538				
Petrale sole CPUE[2]									
4.89	6.31	7.66	11.12	11.31	12.23	13.16	13.61	20.96	23.64
26.31	26.79	28.58	30.07	43.87	56.49	71.43	81.08	94.30	103.02
112.71	115.48	153.96	169.52	179.83	199.80	205.71	310.82	398.51	4635.18

[1] The data set also includes 24 zeros.
[2] Ten zeros are not shown.

$$\text{var}_{est}(c) = \exp(0.350)\left\{g_{50}^2(1.961) - g_{50}(3.841)\right\}$$
$$= 1.42\left\{(6.39)^2 - 34.07\right\} = 9.7.$$

Thus the estimated standard error of c is 3.1 $(= (9.7)^{1/2})$ as compared with an expected value of 3.8 (from Equation 6, $p = 1$). For further examples of the performance of the estimators on lognormal data, see Aitchison and Brown (1957), Blackwood (1991), McConnaughey and Conquest (1992) and Conquest et al. (1996).

The next three examples are survey data that are similar in appearance to the artificial data set in that each contains a single large isolated catch. The first data set is from a trawl survey in the southeastern Bering Sea in 1991. In Table 1 is shown the survey catch per unit of effort (CPUE) of male red king crab, *Paralithodes camtschatica*, of legal size. The largest CPUE is six times greater than the second largest value and accounts for nearly 50% of the total survey catch. In Table 2 the estimates of the mean and the standard errors are calculated as above. The pattern of the estimates is similar to that for the artificial data. In particular, the estimate of the mean, c = 545.0, is much smaller than the sample mean (864.8) and appears to be more precise. The reason that c is so much lower than $\bar{x}$ is that, based on the Δ-lognormal model of the data, a CPUE as large or larger than the biggest value (32,538) would have occurred for approximately 1 in 2,200 tows during the 1991 crab survey, and c weighs the value accordingly. In contrast, the sample mean gives each CPUE value equal weight.

In Table 1, CPUE data are given for petrale sole, *Eopsetta jordani*, from a 1992 trawl survey off the west coast of the United States. The largest catch is 65% of the total catch and is 12 times larger than the next largest catch. Estimates of the mean and standard errors are given in Table 2.

The last example of this type of data set is from a trawl survey off the east coast of the United States. The data (Sissenwine, 1978) are the catch per tow in 1973 of Atlantic mackerel, *Scomber scombrus*. The largest catch (5,182 kg) is more than 25 times greater than the next largest (194 kg) and is 92% of the total catch. This is the one example presented for which lognormality of the nonzero values was rejected (P=0 .02). Though the estimate c = 2.0 kg/tow is considerably smaller than the sample mean ($\bar{x}$ =26.2 kg/tow), it is much more consistent with previous and subsequent survey indices (e.g. 1.6 kg/tow in 1972 and 2.5 kg/tow in 1974) than is the sample mean (see Fig. 5 in Sissenwine, 1978).

No dominating large catch

The more usual type of survey data set is one that is highly skewed but does not contain a relatively large isolated value. A typical example of this sort of data is seen in Figure 2 which shows the catch per tow of juvenile Arcto-Norwegian cod, *Gadus morhua*, collected during a 1989 midwater trawl survey in the western Barents Sea (Helle, 1994). The estimate of the mean from c is 55.2 and from $\bar{x}$ is 49.7. Similarly, the estimate d is greater than the sample variance (Table 2).

Another example is from a 1989 zooplankton survey in the Barents Sea (Helle, 1994). Figure 3 is a plot of the biomass per tow of copepods sampled with a Juday plankton net. The frequency distribution is similar to that in Figure 2, and, again, the estimates c and d are larger than the ordinary sample estimates (Table 2).

The sample average and variance will be underestimates for most samples (i.e. be smaller than the true values). This is due to the sampling distribution of $\bar{x}$ and $s_{\bar{x}}^2$, which, for a highly skewed distribution, will still be skewed to the right for small to

Table 2

Summary statistics for estimating the mean and standard errors for six data sets, where n is the sample size, m is the number of nonzeros, $\bar{x}$ is the sample mean, se_s is the sample standard error (SE), se_d is the SE based on a lognormal model, $\bar{y}$ and s^2 are the mean and variance of the nonzero logged values, c is the estimate of the mean based on a lognormal model, and $[var_{est}(c)]^{1/2}$ is its estimated standard error. The expected or true values for the artificial data are in parentheses.

Data set	n	m	$\bar{x}$	se_s	se_d	$\bar{y}$	s^2	c	$[var_{est}(c)]^{1/2}$
Artificial	50	50	38.8 (7.4)	35.6 (7.6)	5.0 (7.6)	0.175 (0)	3.921 (4)	7.6 (7.4)	3.1 (3.8)
Red king crab	80	56	864.8	415.0	156.0	5.755	1.866	545.0	134.8
Petrale sole	40	30	179.2	115.2	46.9	3.96	2.238	112.1	39.8
Atlantic mackerel	216	67	26.2	24.0	1.4	–0.165	4.269	2.0	0.8
Juvenile cod	161	99	49.7	11.7	26.7	2.759	3.572	55.2	16.4
Zooplankton	160	160	478.1	68.9	93.2	5.338	1.876	525.7	77.2

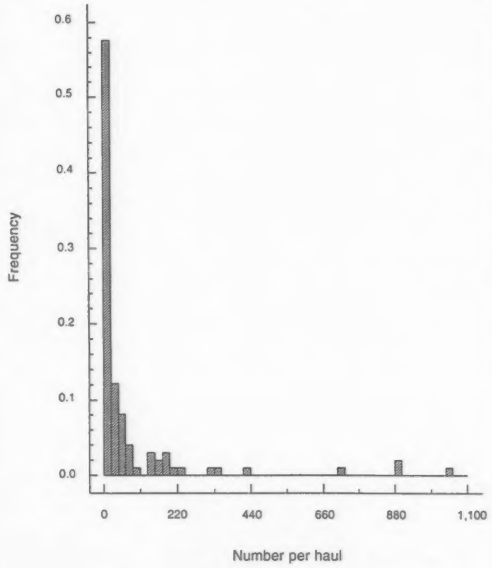

Figure 2

Frequency plot of the number per tow of juvenile Arcto-Norwegian cod from a 1989 midwater trawl survey in the Barents Sea (Helle, 1994). There were also 62 zeros (n=161) which are not included in the plot.

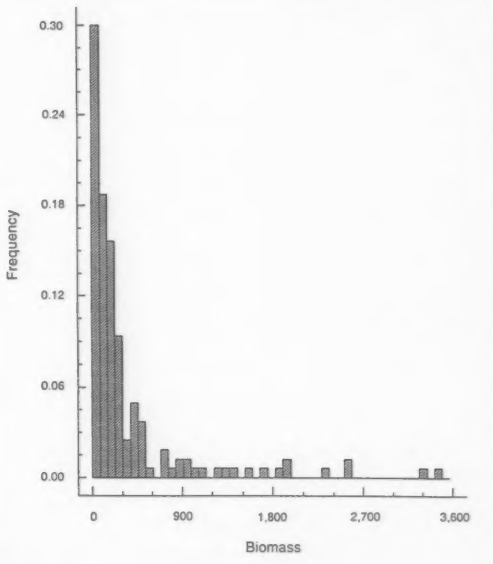

Figure 3

Biomass ($\mu g/m^3$) per tow of copepods *Calanus finmarchicus* and *Oithona similis*. Data are from a 1989 plankton survey in the Barents Sea (Helle, 1994). There were no zero values (n=160).

moderate sample sizes. The median can be much smaller than the mean for a skewed distribution, and, therefore, the sample estimators are not only less efficient but will underestimate the true values of the parameters most of the time (Pennington, 1983; McConnaughey and Conquest, 1992; Conquest et al., 1996). The sampling distribution of s_x^2 is much more skewed than is the sampling distribution of $\bar{x}$, which is the reason that s_x^2 often greatly underestimates its expected value more often than does $\bar{x}$ (Pennington, 1986). The sample estimators are unbiased, even though most of the time the estimates are low and are very high for the occasional sample that contains a huge catch (McConnaughey and Conquest, 1992).

Discussion

The estimators of abundance, based on the lognormal model, perform as expected on real survey data if the underlying model for the nonzero values is a lognormal distribution. The estimates are more precise, and the occasional huge catch does not affect the estimates nearly as much as it does the sample average (see also McConnaughey and Conquest, 1992). The Δ-estimators treat these large catches as part of the distribution, as a reflection of how fish are actually distributed spatially, eliminating the need to handle them as "outliers," that is, to discard the points arbitrarily in an analysis of the data. Since all models only approximate reality, an advantage in using lognormal-based estimators for marine data is that they appear to be fairly robust to deviations from the model (Blackwood, 1991; Pennington, 1991; Conquest et al., 1996).

The Δ-estimators can be much more efficient than the sample estimators but lose this advantage for small samples (see Smith, 1988; Fig. 1). Thus for stratified surveys in which the region is divided into many relatively small strata and only a few stations are selected in each stratum, little would be gained by using the Δ-estimators (Smith, 1988). Only a slight gain in precision is usually achieved by increasing the number of strata beyond 6 (Cochran, 1977). Consequently it appears that a better survey design would be one that has larger strata with at least 20–30 stations in each stratum (Fig. 1). Not only would this design improve the efficiency of the Δ-estimators but it would then be possible to exploit optimal sample allocation schemes that may be more efficient (Gavaris and Smith, 1987; Polacheck and Vølstad,

1993). For current surveys with sampling intensity proportional to stratum area, it would likely be better to combine the small strata into ones with larger sample sizes for calculating abundance estimates. Another way to increase sample sizes for future surveys and to improve survey efficiency in general would be to reduce tow duration and use the time saved to sample at more stations (Pennington and Vølstad, 1991, 1994).

It has been suggested that since the lognormal model may be incorrect or not robust, the sample average and variance are the preferred estimators (Jolly and Hampton, 1990; Myers and Pepin, 1990; Smith, 1990). Using finite population techniques, Smith (1990) examined the performance of the estimators based on the Δ-distribution and concluded that for small populations the estimators are biased and not robust to deviations from the model. But the sort of model-based bias that Smith considered is not a concern for marine surveys. Because for most, if not all, marine surveys, the population size, i.e. the total number of tows that could be made, is effectively infinite, whereas Smith's simulations were samples from populations of size 30. There is no reason that the Δ-estimators should be unbiased if applied to samples from small populations. For Smith's simulations, the usual properties of the lognormal-based estimators are apparent if the small samples (n=3) are assumed to be from a larger population. That is, if the samples of size 3 are assumed to come from a survey for which the possible number of tows (the population size) is large, then the estimators are unbiased (see Table 1 in Smith, 1990). The model-based bias that Smith observed is a function of population size, not a property as such of the Δ-estimators or the size of the sample.

What would cause concern is the possiblity that the underlying distribution may have appeared to be approximately lognormal but was not and that the departure from lognormality caused the lognormal-based estimates and inferences to be misleading. Myers and Pepin (1990) have claimed, motivated by some simulations, that lognormal-based estimators are very sensitive to undetectable deviations from lognormality. But to test a model fairly, the alternative models should be realistic. The nonrobustness that they observed was simply due to the contamination of lognormal distributions with very small values, the opposite of what causes the imprecision of abundance estimates from marine surveys, i.e. the large catches (Pennington, 1991). It was not only that the contaminating values were small, but there was a relatively high probability that small values would occur. Since $\ln x$ goes to minus infinity as x approaches zero, these small values resulted in large negative values on the log scale, which caused the extreme instability of the lognormal-based estimators in Myers and Pepin's simulations. Aitchison (1986, p. 270) made the same point when discussing a sensitivity analysis of another log-based procedure. Analyzing artificial data is no different from analyzing real data; all aspects of the simulated data should be examined carefully (see, e.g. McConnaughey and Conquest, 1992) to ensure that the resulting conclusions are relevant.

In practice, even if such small values were statistically "undetectable" (Myers and Pepin, 1991), one would know (e.g. by looking at the data) whether values could be arbitrarily close to zero and, if so, deal with them appropriately as in Pennington (1991). The small values that may occur after transforming abundance data for a particular length class with an age–length key (Myers and Pepin, 1991) will not cause any problems if the original catch at length data are distributed lognormally. This is because $\ln(ax) = \ln a + \ln x$, and, therefore, the log-based estimate of the mean of ax is a multiplied by that for x.

The reason most often given for using the sample estimates and not employing any modeling techniques is that the sample average and variance are always unbiased estimators (Myers and Pepin, 1990; Smith, 1990). Lognormal-based estimators may be slightly biased for some applications but they are not overly influenced by the occasional huge catches and therefore can have a considerably smaller mean square error than the sample estimates for highly skewed distributions (Conquest et al., 1996).

There are problems if the sample estimates are used for marine data (Lo et al., 1992). The estimators are very sensitive to large catches and therefore may be rather inefficient. Another difficulty is that for the sample sizes common for marine surveys, the distribution of the sample average may be far from normal for these highly skewed distributions (Sissenwine, 1978; McConnaughey and Conquest, 1992; Conquest et al., 1996). Thus the central limit theorem cannot be invoked to assess the uncertainty associated with the estimates or to make inferences. Likewise, the distribution of the Δ-estimator may not approximate a normal distribution for small samples, but for skewed distributions it appears to converge to normality more quickly than does the sample mean (Conquest et al., 1996). For small to moderate sample sizes, methods based on the lognormal model can be used to make confidence statements.

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Origin and genetic structure of chinook salmon, *Oncorhynchus tshawytscha*, transplanted from California to New Zealand: allozyme and mtDNA evidence

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Abstract.—Chinook salmon, *Oncorhynchus tshawytscha*, transplanted from the Sacramento River, California, to the Waitaki River catchment of New Zealand at the turn of the century rapidly colonized many South Island rivers. Allozyme genotype and mtDNA haplotype frequencies were obtained from tissue samples from chinook salmon in Waitaki, Rakaia, Waimakariri, and Clutha rivers in New Zealand and compared with data from populations in the Sacramento River to provide further information on the origin of the NZ populations and to ascertain the genetic changes that have taken place since the transplant. Neither allozyme nor mtDNA unequivocally identified an ancestral "seasonal" run (fall, winter, or spring) for the NZ chinook salmon. Sacramento River samples collectively diverged from the NZ samples at allozyme loci, and mtDNA indicated greater similarity between NZ samples and fall-run rather than winter and spring runs from the Sacramento River. Significant variation was detected by mtDNA analysis between only two of the four populations within NZ, one of which has been landlocked by an impassable dam since 1956. The allozyme data identified significant variation within NZ, although less than has been documented among Sacramento River populations. The NZ populations also showed less genetic diversity (mean number of alleles per locus, proportion of loci that were polymorphic, and mean heterozygosity) than the Sacramento River populations. These lower values are consistent with a population bottleneck in the first generations after transplantation into the Waitaki River catchment and with founder effects during the formation of populations in the other NZ rivers. The combination of genetic differences and phenotypic variation among the NZ populations indicates that Pacific salmon populations can develop rapidly after colonizing suitable habitat.

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Fishery Bulletin 94:506–521 (1996).

Salmonids display great interpopulation variation in life history traits, structure, behavior, and other characteristics, reflecting differences in rearing conditions and genetic adaptation to local environments (Ricker, 1972; Saunders, 1981; Taylor, 1991). Fisheries management attempts to be population-specific, reflecting the importance attached to these adaptations (e.g. McDonald, 1981). The past few years have seen a series of reports documenting losses of discrete Pacific salmon populations in the U.S. Pacific Northwest (Nehlsen et al., 1991; Alkire[1]) and in particular states (Washington: Palmisano et al.[2];

[1] Alkire, C. 1993. The living landscape. Vol. 1: Wild salmon as natural capital. Vol. 2: Pacific salmon and Federal lands. The Wilderness Society, Seattle, WA, 174 p.

Washington Dep. Fisheries[3]; Oregon: Lichatowich, 1989; Nickelson et al.[4]; Kaczynski and Palmisano[5]; California: Brown et al., 1994). The listing of certain populations of chinook, *Oncorhynchus tshawytscha*, and sockeye, *O. nerka*, salmon under the U.S. Endangered Species Act has further focused attention on the concepts of population differentiation and local adaptation (Waples, 1995).

Despite the importance of the "stock concept" in salmon management and the abundant examples of variation among populations, there is little direct information on genetic differentiation through the processes of selection and drift. Transplants, however, provide an opportunity to study these processes. Salmonid transplants, undertaken since at least the middle of the last century, have met with mixed success. Freshwater populations have been very widely established outside the native range of such species as brook trout, *Salvelinus fontinalis* (MacCrimmon and Campbell, 1969) and rainbow trout, *O. mykiss* (MacCrimmon, 1971), but anadromous populations have proven difficult to establish inside or outside the species' endemic range (Withler, 1982; Fedorenko and Shepherd, 1986; Harache, 1992). For example, anadromous sockeye salmon, rainbow trout (steelhead), and Atlantic salmon (*Salmo salar*) have established only freshwater populations in New Zealand (McDowall, 1990), and the pink salmon (*O. gorbuscha*) transplant to Newfoundland was unsuccessful (Lear, 1980). The most long-standing, successful establishment of an anadromous salmonid outside its native range has been the transplant of chinook salmon to New Zealand (NZ) (Fedorenko and Shepherd, 1986; Harache, 1992).

Between 1900 and 1906, chinook salmon embryos, probably originating from Battle Creek, a tributary of the Sacramento River (Fig. 1), were shipped to a hatchery on the Hakataramea River, a tributary of the Waitaki River (Fig. 2) on the South Island of NZ (McDowall, 1994). Within about 10 years, chinook salmon had established self-sustaining runs in other major rivers on the east coast of the South Island up to 230 km away (McDowall, 1990). No subsequent introductions were made, thus NZ chinook salmon developed from a discrete parent stock, relatively free from hatchery influence. The Battle Creek population has been maintained at the Coleman Hatchery (Cope and Slater, 1957); thus we had the opportunity to compare the genotypes of this and other Sacramento River populations with the NZ chinook salmon. In addition, chinook salmon from NZ rivers differ from each other in important, heritable life

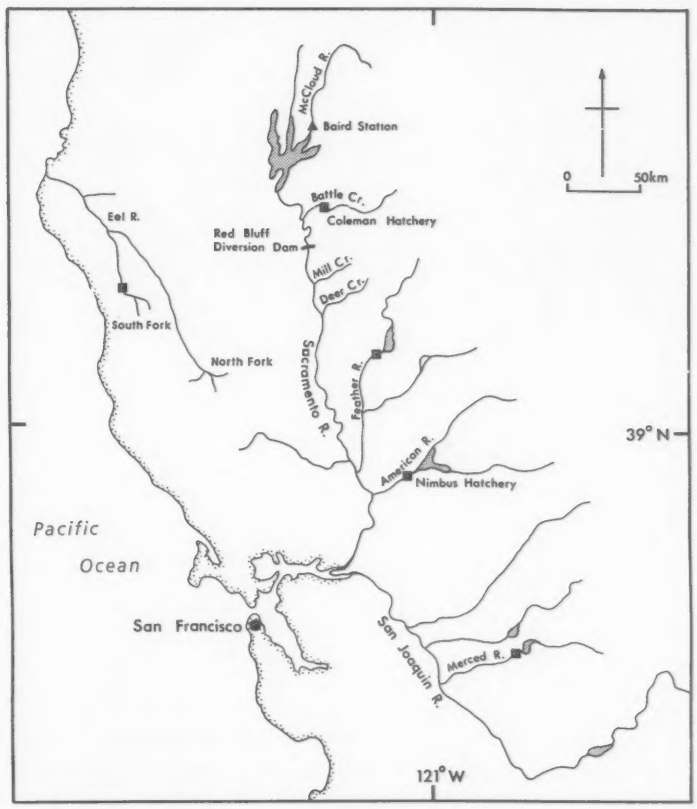

Figure 1

Map of the Sacramento River drainage showing the locations of populations of chinook salmon, *Oncorhynchus tshawytscha*, used in the genetic comparison with New Zealand populations.

[2] Palmisano, J. F., R. H. Ellis, and V. W. Kaczynski. 1993. The impact of environmental and management factors on Washington's wild anadromous salmon and trout. Washington Forest Protection Association and Washington Department of Natural Resources.

[3] Washington Department of Fisheries, Washington Department of Wildlife and Western Washington Treaty Indian Tribes. 1993. 1992 Washington State Salmon and Steelhead Stock Inventory, Olympia, WA, 211 p.

[4] Nickelson, T. E., J. W. Nicholas, A. M. McGie, R. B. Lindsay, D. L. Bottom, R. J. Kaiser, and S. E. Jacobs. 1992. Status of anadromous salmonids in Oregon coastal basins. Oregon Dep. Fish and Wildlife, 83 p.

[5] Kaczynski, V. W., and J. F. Palmisano. 1993. Oregon's wild salmon and steelhead trout: a review of the impact of management and environmental factors. Oregon Forest Industries Council, 328 p.

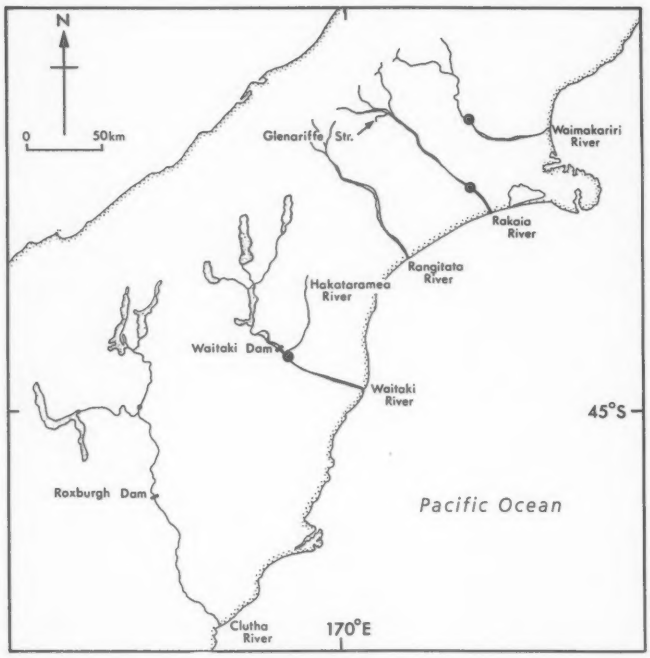

Figure 2

Map of the South Island of New Zealand showing the locations of populations of chinook salmon used in the genetic analysis.

history traits (Quinn and Bloomberg, 1992; Quinn and Unwin, 1993), raising the possibility that genetically distinct populations have evolved within about 20–25 generations and presenting the opportunity for an in-depth study of salmon population differentiation.

Genetic differentiation among populations may arise through selection regimes operating on heritable traits and through genetic drift at the time of colonization (founder effects) and after colonization. Examination of traits not subject to strong selection can provide insights into the importance of genetic drift. Allelic variation at protein-coding loci detected by protein electrophoresis, and more recently, direct examinations of mitochondrial (mt) and nuclear DNA have provided valuable sources of largely neutral molecular genetic markers that permit estimates of degrees of divergence among populations (e.g. Utter, 1991; Carvalho and Pitcher, 1994). Such techniques have helped identify source populations (Hendry et al., in press) and have shown differences between transplanted populations and their source population (Gharrett and Thomason, 1987; Ward et al., 1994) or differences among populations founded by colonization in the new habitat (Krueger and May, 1987). However, population divergence after transplantation is not always detected (Snowdon and Adam, 1992).

There is a substantial database for protein-coding loci on North American chinook salmon (e.g. Utter et al., 1989, 1992; Bartley and Gall, 1990; Bartley et al., 1992), including the Battle Creek population, and a growing database of mtDNA variation (Nielsen et al., 1994, a and b). These two types of data can be more powerful than either alone for studying relatively recent colonization events (Wade et al., 1994). The purposes of the present investigation were to use variation at protein-coding loci and mtDNA to investigate 1) the nature of the founding population (e.g. fall, winter, or spring), 2) whether NZ fish differ in gene frequencies from the descendants of the source population, 3) whether NZ populations differ from each other, and 4) whether NZ fish differ in the levels of genetic variation from descendants of the source population.

Materials and methods

History and origins of NZ chinook salmon

The first shipment of fertilized chinook eggs to NZ was collected from spring-run adults captured in the McCloud River, a tributary of the upper Sacramento River (Fig. 1), 2–27 Sept. 1875 (United States Commission of Fish and Fisheries, 1874–1901). Subsequent shipments of 100,000–500,000 chinook embryos from Baird Station on the McCloud River to the South Island continued to the end of the century, but no self-sustaining populations were established and records of even isolated individual salmon are subject to doubt (McDowall, 1994). There were apparently five shipments from California in the 1900's, arriving in NZ in January–February 1901 (500,000 embryos), 1904 (300,000), 1905 (300,000), 1906 (500,000), and 1907 (500,000; McDowall, 1994). McDowall (1994) concluded that the shipment which arrived in 1904 produced the first returns to the Hakataramea Hatchery in 1907 and that this and the subsequent shipments founded the NZ runs. These embryos were shipped from Battle Creek, but it is unclear whether they originated from Mill Creek or Battle Creek.

Collection of samples

Juvenile salmon (100 per population) were collected from the Waimakariri, Rakaia, and Waitaki rivers

(Fig. 2), three of the four major salmon-producing rivers in NZ (McDowall, 1990). Collection sites in the Waimakariri, Rakaia, and Waitaki rivers were 55, 18, and 57 km above the river mouths, respectively. All collections were made in mid-late summer (12 January to 2 February 1993), early enough in the season to ensure that both ocean-type and stream-type juveniles (Healey, 1991) would have been present (Hopkins and Unwin, 1987; Unwin and Lucas, 1993). Mean fork lengths (FL) ranged from 61 mm (Waitaki) to 76 mm (Waimakariri). Only 63 parr were caught in the Rakaia River mainstem, so another 38 (83 mm mean FL) were collected from the downstream trap on Glenariffe Stream, a major spawning tributary 94 km upstream from the mouth (Unwin, 1986). We also sampled 62 landlocked adults (409 mm mean FL) from Lake Dunstan, a hydroelectric impoundment in the upper Clutha River formed in 1992.

Allozyme analysis

Samples collected from NZ were frozen on dry ice and transported to the National Marine Fisheries Service Auke Bay Laboratory where they were stored at –80°C. Tissue extraction and protein electrophoresis procedures followed those described in Aebersold et al. (1987). Following initial screening for activity and variation at 71 loci, 24 polymorphic loci (Table 1) were selected for comparison with parallel allelic data reported for five Sacramento River populations by Bartley et al. (1992): fall chinook salmon from the Coleman Hatchery (Battle Creek), the Nimbus Hatchery (American River), and the Feather River Hatchery (all on tributaries of the lower Sacramento River); fall chinook salmon from the Merced River Hatchery on a tributary of the San Joaquin River; and wild winter-run chinook salmon from the upper Sacramento River. To provide additional perspective on the levels of genetic variation observed, we also analyzed data on fall chinook salmon from the South Fork of the Eel River, which enters the Pacific Ocean north of the Sacramento River (Bartley et al., 1992; Fig. 1). Compatible data within a subset of 10 out of the 24 polymorphic loci for three Sacramento River samples (Coleman Hatchery fall-run and both fall-run and spring-run from the Feather River Hatch-

Table 1

List of names and Enzyme Commission (E.C.) numbers of variable enzymes, and of designations, tissue distributions (E=eye, H=heart, L=liver, M=skeletal muscle, listed in sequence of optimal resolution) and relative mobilities of variant allelic forms of polymorphic loci.

Enzyme name	E.C. no.	Locus	Relative mobilities of variants	Tissue distribution
Aspartate aminotransferase	2.6.1.1	*mAAT-1**	-104	M, H
		*mAAT-2**	-125, -90	M, H
Adenosine deaminase	3.5.4.4	*ADA-1**	83, 108	M, E, H
Aconitate hydratase	4.2.1.3	*sAH**	86, 112	L
		*mAH-4**	119, 112	L
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-B2**	60, 135	M
		*GPIr**	[1]	M
Glutathione reductase	1.6.4.2	*GR**	110	M, E, H, L
Hydroxyacylglutathione hydrolase	3.1.2.6	*HAGH**	65	M, H, L
L-iditol dehydrogenase	1.1.1.14	*IDDH-2**	61	L
Isocitrate dehydrogenase	1.1.1.27	*mIDHP-2**	150	M, E
		*sIDHP-1**	142, 83	M, H, E, L
		*sIDHP-2**	127, 50, 83, 66	H, E, L
Malate dehydrogenase	1.1.1.37	*sMDH-B2**	121, 70, 126	M, H, L
Malic enzyme	1.1.1.40	*sMEP-1**	78	M, H
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	109	M, H, E
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	90	M, E, H
Phosphoglucomutase	5.4.2.2	*PGM-2**	166	M, H, L
Phosphoglycerate kinase	2.7.2.3	*PGK-2**	90, 74	M, E, L
Dipeptidase	3.4.- -	*PEP-A**	90	M, E, H, L
Proline dipeptidase	3.4.- -	*PEP-D2**	107	M, H
Tripeptide aminopeptidase	3.4.- -	*PEP-B2**	108	M, H
Triose-phosphate isomerase	5.3.1.1	*TPI-2.1**	104, 106	M, E, H
		*TPI-2.2**	102	M, E, H

[1] Allele was detected by the absence of a heteromeric band between *GPI-A** and *GPI-B1** subunits (see Utter et al., 1989).

ery) reported in Utter et al. (1989) were also included 1) to provide data for spring-run fish from the Feather River Hatchery that were not examined by Bartley et al. (1992) and 2) for comparison among different year classes of fall-run fish. Genetic nomenclature followed Shaklee et al. (1990).

Genetic data for NZ and California populations were analyzed with the BIOSYS-1 program[6] to calculate pairwise measures of genetic distances (Cavalli-Sforza and Edwards, 1967; Nei, 1972), gene diversity (F_{ST}, Wright, 1969), chi-square comparisons of heterogeneity, and to construct phenograms through the unweighted pair-group method (Sneath and Sokal, 1973). A neighbor-joining tree (Saitou and Nei, 1987) was constructed from a matrix of arc distances (from Cavalli-Sforza and Edwards [1967]) through the NTSYS-pc program (Rohlf, 1994). Conformance of genotypic proportions of NZ collections to those expected under Hardy-Weinberg (binomial) equilibrium was tested by Levene's (1949) formula for small sample size; the variant alleles were pooled in tests involving loci with more than two alleles.

mtDNA analysis

Total genomic DNA was extracted from a small section of caudal fin tissue from 172 juvenile NZ salmon with Chelex-100 (Walsh et al., 1991) according to the protocol in Nielsen et al. (1994a). A 2-µL aliquot of the chelex-treated supernatant containing salmon DNA was used as a template for amplification with the polymerase chain reaction (PCR) and conserved primers. Our PCR protocol used primers (S-phe and P2; sequences in Nielsen et al., 1994a) that amplify a highly variable segment of the mtDNA control region in salmonids. Amplification, purification, and sequencing of salmon mtDNA were done according to the protocol in Nielsen et al. (1994a). Sequencing reactions were separated in linear 9% polyacrylamide-7 M urea gels and were autoradiographed for 24 to 72 h at room temperature. Mitochondrial DNA sequences were scored with base-pair (bp) differences found within the amplified control region sequence (Nielsen et al., 1994a).

Data on NZ chinook salmon mtDNA sequence frequencies were compared with data from Sacramento River chinook salmon with known spawning seasons (Nielsen et al., 1994b) as follows: winter-run: 72 fish taken from 1991 to 1993 broodstock program at the Coleman Hatchery; fall-run: 359 fish taken from 1992 to 1994 at hatcheries on the American, Merced, and Feather rivers; and spring-run: 32 wild fish collected in Deer and Mill creeks (1991–93) and 27 adults from the Butte Creek spring-run population (1994).

To test for differences in mtDNA frequency among the NZ chinook salmon populations and between the NZ and Sacramento River runs we used an unbiased estimate of Fisher's exact test for population differentiation with a Markov chain analysis (GENEPOP[7]). The Markov model in GENEPOP was run with 4 seeds for the pseudo-random number generator, and the dememorisation number was set to 1,000, the number of batches to 50, and with the number of iterations/batch to 1,000.

Results

Protein-coding loci: genetic variation within populations

Tests for conformance to Hardy-Weinberg genotypic proportions in the NZ populations indicated no deviation from proportions expected in a random mating population. Two tests out of 42 deviated significantly from expected proportions at the 5% level of significance; deficiencies of heterozygotes were observed for *sAH** in the Waimakariri and for *PEPA** in the Waitaki populations. This proportion of deviations (0.048) would be expected by chance at this level of significance. Similar findings were reported by Bartley et al. (1992) for wild California populations, although somewhat higher rates of deviation occurred among hatchery samples. No deviations with Sacramento River samples were reported in Utter et al. (1989). Levels of genetic variation were generally higher in the Sacramento River collections than in the NZ or South Fork Eel River samples (Table 2). The highest mean number of alleles per locus, percentage of loci polymorphic, and mean heterozygosity were seen in the Sacramento River collections, and no overlap in percentage of polymorphic loci occurred between these and any of the other collections.

Protein-coding loci: genetic variation among populations

Allele frequencies at 24 polymorphic protein-coding loci (Table 3) varied considerably among populations. The gene diversity among populations (F_{ST}) averaged

[6] Swofford, D. L., and R. B. Selander. 1989. BIOSYS-1: a computer for the analysis of allelic variation in population genetics and biochemical systematics, release 1.7. Illinois Natural History Survey, 43 p.

[7] Raymond, M., and F. Rousset. 1994. GENEPOP, version 1.0, January 1994. Available through M. Raymond, Laboratoire de Génétique et Environnement, URA CNRS 327, Place E. Bataillon, 34095 Montpellier cedex 05, France. E-mail: Raymond@univ-montp2.fr.

Table 2

Genetic variability at 24 polymorphic protein-coding loci of chinook salmon from rivers in the Sacramento River drainage and South Eel River, California (CA), and from New Zealand (NZ). A locus was considered to be polymorphic if the frequency of the most common allele did not exceed 95%. Mean heterozygosity was the Hardy-Weinberg expected value (Nei, 1978). Standard errors are in parentheses. CA data are from Bartley et al. (1992).

Population	Mean sample size per locus	Mean no. of alleles per locus	% of loci polymorphic	Mean heterozygosity
Battle Creek, CA	100.0	2.1 (0.1)	58.3	0.156 (0.032)
Merced River, CA	100.0	1.8 (0.1)	46.2	0.141 (0.029)
Feather River, CA	100.0	2.0 (0.1)	50.0	0.151 (0.032)
American River, CA	100.0	2.0 (0.1)	58.3	0.164 (0.032)
Upper Sacramento River, CA	94.0	1.9 (0.1)	45.8	0.142 (0.033)
South Eel River, CA	95.8	1.6 (0.1)	29.2	0.113 (0.035)
Rakaia River, NZ	80.9	1.7 (0.1)	29.2	0.111 (0.033)
Waimakariri River, NZ	77.3	1.9 (0.1)	41.7	0.137 (0.032)
Waitaki River, NZ	67.1	1.8 (0.1)	33.3	0.117 (0.033)

over all loci was 0.051, and ranged among individual loci from 0.002 for *mAAT-2** and *PEP-D2** to 0.217 for *GPI-B2** (Table 4). Matrices of pairwise comparisons of two measures of genetic distance (Cavalli-Sforza and Edwards, 1967; Nei, 1972) among populations (Table 5) provided the basis for identifying possible distinct population groupings reflected in this diversity. The UPGM projection of pairwise measures of Nei's distance (Fig. 3A) separated the South Fork Eel River fish from the remaining collections. Two subgroups, comprising the Sacramento and NZ populations, were also apparent. In the Sacramento River subgroup, the Merced Hatchery (San Joaquin River) fall-run fish diverged from the Battle Creek (Coleman Hatchery), Feather River, and American River (Nimbus Hatchery) fall-run fish and from the wild Sacramento River winter-run fish. The three NZ populations grouped more closely within their subgroup than did the Sacramento River populations within theirs. The matrix of Cavalli-Sforza and Edwards distances (Table 5) revealed a comparable UPGM clustering (not pre-

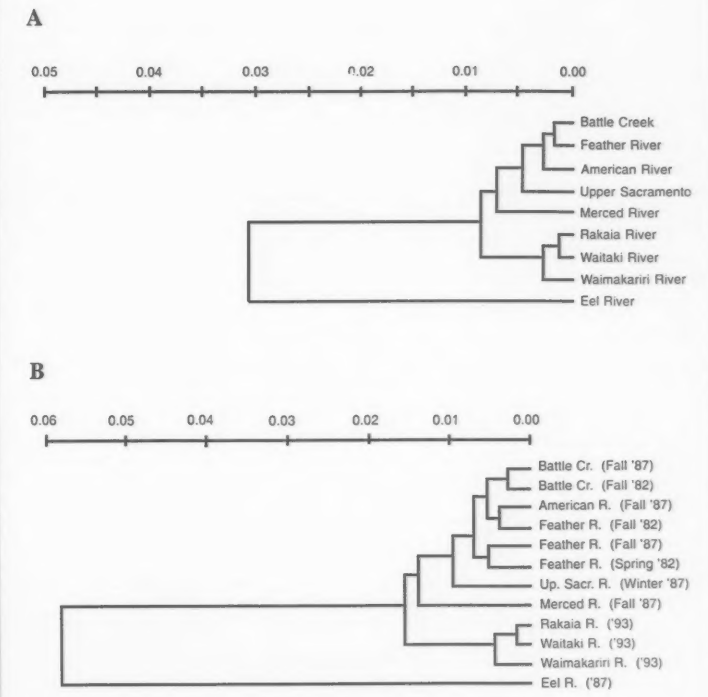

Figure 3

UPGM phenograms of chinook salmon populations from California and New Zealand based on pairwise Nei's (1972) relative genetic distance measures. (**A**) Data from 24 polymorphic loci for collections 1–9. (**B**) Data from 10 polymorphic loci for collections 1–12 (see Table 4 for details).

Table 3

Allele frequencies of 24 polymorphic protein-coding loci for chinook salmon collections (year follows in parentheses) from California: 1 = Battle Creek, fall-run (1987); 2 = Merced River, fall-run (1987); 3 = Feather River, fall-run (1987); 4 = American River, fall-run (1987); 5 = Upper Sacramento River, winter-run (1987); 6 = South Eel River, fall-run (1987) and New Zealand; 7 = Rakaia River (1993); 8 = Waimakariri River (1993); and 9 = Waitaki River (1993). Data for collections 1–6 are from Bartley et al. (1992). Additional California data for 10 loci (from Utter et al., 1989) are provided: 10 = Feather River, spring-run (1982); 11 = Battle Creek fall-run (1982); and 12 = Feather River, fall-run (1982).

	Collection											
Locus	1	2	3	4	5	6	7	8	9	10	11	12
mAAT-1*												
(*n*)	100	100	100	100	94	98	80	83	80			
**100*	0.960	1.000	0.975	1.000	0.995	1.000	1.000	1.000	1.000			
**-104*	0.040	0.000	0.025	0.000	0.005	0.000	0.000	0.000	0.000			
*mAAT-2**												
(*n*)	100	100	100	100	94	46	80	83	80			
**100*	0.995	1.000	0.995	1.000	1.000	0.989	1.000	0.982	1.000			
**-125*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**-90*	0.000	0.000	0.005	0.000	0.000	0.011	0.000	0.018	0.000			
ADA-1*												
(*n*)	100	100	100	100	94	99	81	83	23	50	300	200
**100*	1.000	0.870	0.955	0.960	1.000	1.000	1.000	0.982	0.978	1.000	0.999	1.000
**83*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.012	0.000	0.000	0.001	0.000
**108*	0.000	0.130	0.045	0.040	0.000	0.000	0.000	0.006	0.022	0.000	0.000	0.000
sAH*												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.775	0.765	0.885	0.835	0.862	0.995	0.778	0.831	0.850	0.720	0.815	0.797
**86*	0.200	0.165	0.105	0.130	0.128	0.005	0.210	0.157	0.131	0.240	0.173	0.195
**112*	0.025	0.070	0.010	0.035	0.011	0.000	0.012	0.012	0.019	0.040	0.012	0.007
mAH-4*												
(*n*)	100	100	100	100	94	99	81	74	55			
**100*	0.925	0.905	0.860	0.925	0.957	0.874	0.938	0.858	0.891			
**119*	0.020	0.065	0.035	0.020	0.011	0.126	0.062	0.142	0.100			
**112*	0.055	0.030	0.105	0.055	0.032	0.000	0.000	0.000	0.009			
GPI-B2*												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.940	0.965	0.925	0.930	0.777	0.535	1.000	1.000	0.994	1.000	0.945	0.900
**60*	0.040	0.035	0.065	0.070	0.064	0.465	0.000	0.000	0.006	0.000	0.055	0.100
**135*	0.020	0.000	0.010	0.000	0.160	0.000	0.000	0.000	0.000	0.000	0.000	0.000
GPIr*												
(*n*)	100	100	100	100	94	99	81	83	79	50	300	200
**100*	0.715	0.755	0.615	0.655	0.644	1.000	0.469	0.392	0.538	0.576	0.705	0.689
**r*[1]	0.285	0.245	0.385	0.345	0.356	0.000	0.531	0.608	0.462	0.424	0.295	0.311
GR*												
(*n*)	100	100	100	100	94	99	81	83	79	50	300	200
**100*	1.000	1.000	1.000	1.000	1.000	1.000	0.981	0.958	1.000	1.000	1.000	1.000
**110*	0.000	0.000	0.000	0.000	0.000	0.000	0.019	0.042	0.000	0.000	0.000	0.000
HAGH*												
(*n*)	100	100	100	100	94	99	81	78	8			
**100*	1.000	1.000	1.000	0.990	1.000	1.000	0.975	0.865	1.000			
**65*	0.000	0.000	0.000	0.000	0.000	0.000	0.025	0.135	0.000			

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Table 3 (continued)

Locus	Collection 1	2	3	4	5	6	7	8	9	10	11	12
IDDH-2*												
(*n*)	100	100	100	100	94	97	81	25	59			
**100*	0.990	0.990	0.975	0.990	0.984	0.985	1.000	1.000	1.000			
**61*	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.000	0.000			
**20*	0.000	0.010	0.025	0.010	0.016	0.000	0.000	0.000	0.000			
mIDHP-2*												
(*n*)	100	100	100	100	94	98	81	69	56			
**100*	0.905	0.885	0.950	0.830	0.941	0.990	1.000	1.000	0.973			
**150*	0.095	0.115	0.050	0.170	0.059	0.010	0.000	0.000	0.027			
*sMDH-B2**												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.920	0.935	0.955	0.905	0.979	1.000	0.957	0.928	0.956	0.945	0.968	0.977
**121*	0.070	0.040	0.045	0.065	0.021	0.000	0.043	0.072	0.044	0.055	0.032	0.023
**70*	0.000	0.025	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
**126*	0.010	0.000	0.000	0.030	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
*sMEP-1**												
(*n*)	100	100	100	100	94	79	81	74	20			
**100*	0.805	0.860	0.810	0.775	0.851	0.557	0.895	0.858	0.775			
**78*	0.195	0.140	0.190	0.225	0.149	0.443	0.105	0.142	0.225			
*MPI**												
(*n*)	100	100	100	100	94	99	81	79	78	50	300	200
**100*	0.585	0.700	0.580	0.545	0.617	0.818	0.556	0.570	0.551	0.510	0.586	0.487
**109*	0.415	0.300	0.420	0.455	0.383	0.182	0.444	0.430	0.449	0.497	0.414	0.513
*PGDH**												
(*n*)	100	100	100	100	94	99	81	83	78			
**100*	0.975	0.900	0.960	0.920	0.979	1.000	0.975	0.976	1.000			
**90*	0.025	0.100	0.040	0.080	0.021	0.000	0.025	0.024	0.000			
*PGM-2**												
(*n*)	100	100	100	100	94	99	81	83	71			
**100*	0.990	1.000	0.995	1.000	0.995	1.000	0.994	0.988	0.972			
**166*	0.010	0.000	0.005	0.000	0.005	0.000	0.006	0.012	0.028			
*PGK-2**												
(*n*)	100	100	100	100	94	99	81	83	71	50	300	200
**100*	0.495	0.670	0.490	0.605	0.590	0.480	0.704	0.705	0.718	0.540	0.592	0.651
**90*	0.505	0.330	0.510	0.395	0.410	0.520	0.296	0.289	0.282	0.460	0.408	0.349
**74*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.000	0.000	0.000	0.000
*PEP-A**												
(*n*)	100	100	100	100	94	99	81	83	80	50	300	200
**100*	0.810	0.950	0.850	0.875	0.894	0.965	0.951	0.952	0.938	0.890	0.869	0.905
**90*	0.190	0.050	0.150	0.125	0.106	0.035	0.049	0.048	0.063	0.110	0.131	0.095
PEP-D2												
(*n*)	100	100	100	100	94	98	81	82	70			
**100*	0.995	1.000	1.000	0.990	1.000	1.000	1.000	1.000	1.000			
**107*	0.005	0.000	0.000	0.010	0.000	0.000	0.000	0.000	0.000			

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Table 3 (continued)

Locus	Collection 1	2	3	4	5	6	7	8	9	10	11	12
*TPI-2.1**												
(*n*)	100	100	100	100	94	99	81	83	76			
*100	0.945	0.830	0.915	0.870	0.936	0.899	0.988	1.000	0.974			
*104	0.055	0.170	0.085	0.130	0.064	0.000	0.012	0.000	0.026			
*106	0.000	0.000	0.000	0.000	0.000	0.101	0.000	0.000	0.000			
*TPI-2.2**												
(*n*)	100	100	100	100	94	99	81	83	80			
**100*	0.930	0.965	0.950	0.960	1.000	0.975	0.988	0.982	1.000			
**102*	0.070	0.035	0.050	0.040	0.000	0.025	0.012	0.018	0.000			
*PEP-B2**												
(*n*)	100	100	100	100	94	99	81	45	69	50	300	200
**100*	0.890	0.955	0.950	0.940	0.862	0.965	0.957	0.900	0.949	0.950	0.842	0.889
**108*	0.110	0.045	0.050	0.060	0.138	0.035	0.043	0.100	0.051	0.050	0.158	0.111
*sIDHP-1**												
(*n*)	100	100	100	100	94	99	81	83	79			
**100*	0.995	1.000	1.000	1.000	0.952	1.000	1.000	1.000	1.000			
**142*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**83*	0.000	0.000	0.000	0.000	0.048	0.000	0.000	0.000	0.000			
*sIDHP-2**												
(*n*)	100	100	100	100	94	99	81	83	79			
**100*	0.905	0.995	0.895	0.875	0.910	0.859	0.914	0.873	0.956			
**127*	0.090	0.005	0.105	0.125	0.085	0.141	0.086	0.120	0.032			
**50*	0.000	0.000	0.000	0.000	0.005	0.000	0.000	0.000	0.000			
**83*	0.005	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000			
**66*	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.006	0.013			

[1] Allele was detected by the absence of a heteromeric band between *GPI-A** and *GPI-B1** subunits (see Utter et al., 1989).

sented), and a neighbor-joining tree (Fig. 4) also displayed similar clustering, that separated the NZ and Sacramento River populations.

Relationships from the subset of 10 polymorphic loci (Fig. 3B) paralleled those indicated with 24 loci (Fig. 3A). Each of the additional three samples from Utter et al. (1989) were grouped within the clustering of Sacramento River collections reported by Bartley et al. (1992). Notably, the spring-run collection from the Feather River Hatchery was indistinct from fall-run collections from the Feather River and from other Sacramento River hatcheries. Furthermore, the stability of allele frequencies at these loci was evident for fall-run fish collected as juveniles in 1982 (Utter et al., 1989) and 1987 (Bartley et al., 1992).

Decreasing heterogeneity among the 24 loci was apparent when chi-square tests within subgroups were contrasted with those involving all collections (Table 4). Within the total grouping, all but two loci were heterogeneous ($P<0.01$). A lower level of significance occurred for 9 loci within the Sacramento River and for all but one locus among the NZ collections. Standardized measures of these differences indicated more than a doubling of heterogeneity for the Sacramento subgroup relative to the NZ subgroup, and a near doubling of the total heterogeneity relative to the Sacramento collections.

Much of the total heterogeneity reflected the distinction of the South Fork Eel River collection from the remaining group, notably owing to allele frequency differences approaching or exceeding 0.4 at *GPI-B2** and *GPIr**, and to only slightly lower distinctions at *sMEP-1**, and *MPI** (see Table 3). Allelic differences between the Sacramento and NZ subgroups were more subtle. Nonoverlapping frequencies at many loci (*GPI-B2**, *GPIr**, *IDDH-2**, *IDH-2**, *PGM-2**, *PGK-2**, *TPI-2.1**) contributed to their differentiation. In addition, some variants in the NZ subgroup were either absent in all the Sacramento subgroups (*GR**) or occurred at a very low frequency

and not in the Battle Creek population (*HAGH**).

Mitochondrial DNA: genetic variation among populations

There were no new base substitutions found in the 171-bp section of the mtDNA control region of the NZ chinook sequence that we sequenced, compared with mtDNA types reported for Sacramento River chinook (Table 1 in Nielsen et al., 1994b). However, because the base change recorded at bp 183 contained a cryptic deletion that was difficult to score consistently in the NZ fish, we pooled mtDNA types 1 and 4 (as previously reported), which were originally differentiated by a single deletion at bp 183. The same cryptic nucleotide deletion was found in haplotype 3 in the NZ chinook; therefore, the base cytosine (C) and the deletion found at this site were pooled for all populations, yielding five mtDNA types used in this analysis (Table 6).

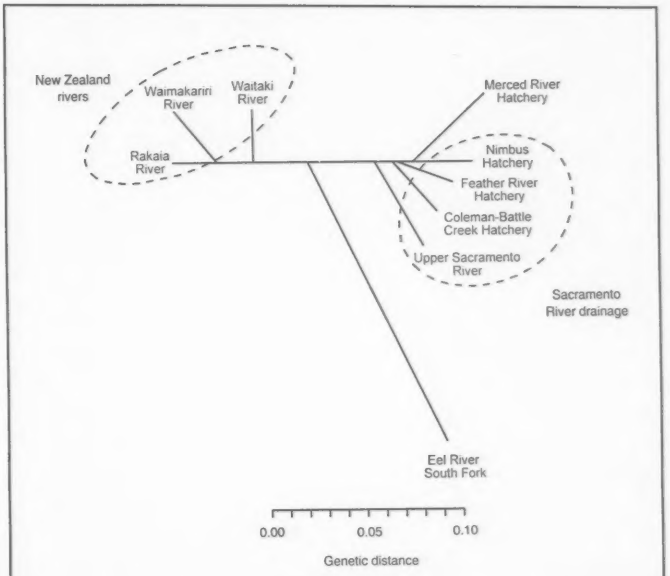

Figure 4

Neighbor-joining tree (Saitou and Nei, 1987) displaying relationships among chinook salmon populations from California and New Zealand based on a matrix of genetic distance measures (Cavalli-Sforza and Edwards, 1967; Table 5). Dashed circles enclose the three New Zealand and four Sacramento River populations.

The NZ salmon populations were dominated by mtDNA haplotype 1, representing 82% in the pooled sample compared with 69% in the Sacramento River population (Table 7). Haplotype 2 was rare in the NZ fish (only one sample was found, from the Waimakariri River) and detected only in fall-run fish from the Sacramento River. Haplotype 3 was detected at low frequencies in NZ and in the Sacramento River fall-run fish. This haplotype was found at higher frequencies in the 1994 spring-run samples taken at Butte Creek and not at all in the Deer and Mill Creeks spring-run collection (1991–93) or the winter-run California chinook. Fish carrying haplotype 5 in the Clutha and Waitaki NZ chinook shared a close frequency distribution to that observed in the Sacramento River fall-run fish. The frequency distribution of haplotype 5 in the Sacramento River fall-run population was primarily due to an increase in its relative abundance in one year class (1994). Haplotype 6 was found only in the winter-run Sacramento fish and not in any NZ population.

The Fisher's exact tests, which compared the total NZ chinook population with each of the three Sacramento River runs of chinook were compared, indicated that the NZ chinook differed significantly from the winter- and spring-run fish ($P<0.001$) but not from the fall-run samples ($P=0.08$). Haplotype frequencies varied among the four NZ populations, but the Clutha River population, with only two mtDNA variants (1 and 5), was the only population to differ ($P<0.01$) from any other population (Rakaia; Table 7).

Discussion

Contrasts among population groups

The allozyme and mtDNA data sets provided complementary and independent comparisons for considering the origin and differentiation of the NZ chinook salmon populations. At the broadest level, the Sacramento and NZ populations share a common lineage (Figs. 3 and 4). The collection from the Eel River, though geographically adjacent to the Sacramento drainage, is typical of a distinct coastal lineage, distinguished by high frequencies of *GPI-2** variation and monomorphism for *GPIr** (Utter et al., 1989; Bartley and Gall, 1990; Bartley et al., 1992). At a finer level, some details of the separate Sacramento and NZ subgroups were apparent from both data sets. The most obvious distinction was the greater degree of divergence among the Sacramento populations on the basis of comparative genetic distances (Table 4; Fig. 3), allelic heterogeneity and partitioning of gene

Table 4

Contingency chi-square (χ^2) analyses and degrees of freedom (df) among all collections (from South Fork Eel River, Sacramento River (CA), and from New Zealand) with data from 24 protein-coding loci, and the Sacramento River and New Zealand subgroups. "—" indicates fixation for common allele in compared group. Significance levels are indicated as follows: ns (P>0.05); * (0.05 > P> 0.01); ** (0.01>P>0.001); *** (P<0.001). Standardized measure is χ^2/df.

	Collections included in analysis								
	Total			Sacramento River			New Zealand		
Locus	χ^2	df	P	χ^2	df	P	χ^2	df	P
*mAAT-1**	40.052	8	***	18.035	4	**	—	—	—
*mAAT-2**	23.833	16	ns	7.886	8	ns	5.819	4	ns
*ADA-1**	117.915	16	***	53.655	4	***	5.731	4	ns
sAH	81.151	16	***	26.092	8	**	4.007	4	ns
*mAH-4**	108.921	16	***	25.984	8	**	8.349	4	ns
*GPI-B2**	606.586	16	***	106.551	8	***	2.054	2	ns
*GPIr**	202.800	8	***	11.804	4	*	6.991	2	*
*GR**	48.936	8	***	—	—	—	7.194	2	*
*HAGH**	168.593	16	***	7.896	4	ns	15.227	2	***
*IDDH-2**	48.413	24	**	13.442	8	ns	—	—	—
*mIDHP-1**	82.834	8	***	20.898	4	***	8.095	2	*
*sMDH-A2**	91.154	24	***	43.336	12	***	1.803	2	ns
*sMEP-1**	80.033	8	***	6.577	4	ns	4.105	2	ns
*MPI**	53.112	8	***	11.540	4	*	0.118	2	ns
*PGDH**	50.497	8	***	19.048	4	***	3.871	2	ns
*PGM-2**	15.185	8	ns	3.503	4	ns	2.6372	2	ns
*PGK-2**	67.987	16	***	19.290	4	***	1.915	4	ns
*PEP-A**	54.293	8	***	19.817	4	***	0.404	2	ns
*PEP-D2**	10.770	8	ns	5.249	4	ns	—	—	—
*TPI-2.1**	237.524	8	***	20.386	4	***	4.452	2	ns
*TPI-2.2**	72.565	16	***	13.327	4	**	2.729	2	ns
*PEP-B2**	29.622	8	***	17.997	4	**	3.624	2	ns
*sIDHP-1**	78.781	16	***	42.576	8	***	—	—	—
*sIDHP-2**	60.541	32	**	22.329	16	**	10.752	4	*
Totals	2,387.107	320	***	548.327	136	***	99.878	50	***
Standarized measure		7.36			4.42			2.08	
F_{ST}		0.051			0.013			0.005	

Table 5

Matrix of genetic distance coefficients based on 24 protein-coding loci. Below the diagonal (****) are estimates of Nei's (1972) genetic distance; above the diagonal are Cavalli-Sforza and Edwards (1967) chord distances.

	Collection								
Collection and site	1	2	3	4	5	6	7	8	9
1 Battle Cr.	****	0.097	0.060	0.067	0.077	0.162	0.100	0.122	0.092
2 Merced R.	0.006	****	0.082	0.072	0.107	0.172	0.111	0.133	0.093
3 Feather R.	0.002	0.006	****	0.059	0.076	0.159	0.098	0.116	0.082
4 Nimbus R.	0.002	0.004	0.002	****	0.091	0.167	0.107	0.127	0.090
5 Upper Sacra. R.	0.003	0.006	0.003	0.004	****	0.162	0.102	0.124	0.092
6 South Eel R.	0.023	0.025	0.023	0.024	0.022	****	0.180	0.190	0.166
7 Rakaia R.	0.007	0.008	0.006	0.006	0.006	0.038	****	0.053	0.063
8 Waimakariri R.	0.011	0.013	0.008	0.009	0.008	0.042	0.002	****	0.085
9 Waitaki R.	0.006	0.007	0.004	0.004	0.005	0.031	0.002	0.003	****

diversity (Table 2). Greater mtDNA haplotype diversity also occurred within the Sacramento subgroup where haplotype 6, detected in winter-run fish, was absent from the NZ fish. These observations comport with the introduction of Sacramento River chinook from a single source to NZ a century ago.

In the NZ collections, the common clustering (Figs. 3 and 4) and generally lower heterozygosities and percentages of polymorphic loci (Table 2) support the occurrence of a limited effective population size (i.e. a "bottleneck") during the founding and perhaps during the early generations of these populations. Enhanced genetic drift resulting from a bottleneck followed by a larger and more stable population size would explain the common clustering of these collections and the lower levels of genetic variation, compared with those observed in the Sacramento River collections. There are no records of population sizes in the first few generations, but natural mortality and the general tendency of salmon to home would have reduced the number of adults colonizing the rivers. Current populations (catch plus escapement) are on the order of 10,000 adults in the four major rivers, including the three sampled in this study.

Several factors might have contributed to the initial bottleneck. The founding population probably represented more females than males, as hatchery staff commonly spawn females with a few "choice" males. The founding individuals experienced a very different environment and presumably a different selection regime from the Sacramento River. The NZ chinook salmon rivers lack the estuary used by fall chinook salmon in the Sacramento River system (Kjelson et al., 1982), and smolts unable to make the abrupt transition to seawater may have died. The surviving smolts of the first generation experienced ocean currents, temperature, and other factors influencing migratory patterns and orientation that differed from those experienced off the coast of California. There may have been strong selection for coastal distribution or other behavior patterns facilitating homeward orientation. Upon return, the mature adults found short, steep, gravel-rich, unstable, recently deglaciated rivers, whose channels lacked woody debris. In addition to these habitat differences that may have exerted selection on the founding generations, the nature of the salmonid mating system (semelparous life cycle and intrasexual competition for nesting sites or mates) also generates considerable variation in reproductive success, especially among males (e.g. Fleming and Gross,

Table 6

Four variable base-pair sites and nucleotide changes found in five chinook salmon mtDNA types from four wild populations in New Zealand and from fish collected in the Sacramento River, California, 1991–93.

MtDNA type	*n*	Variable sites			
		47	125	134	183
1 and 4	479	G	T	C	C/*
2	15	A	T	C	C
3	59	G	T	A	C/*
5	107	G	T	C	A
6	2	G	81i[1]	C	C

[1] The symbol "81i" represents an 81-bp exact repeat. An asterisk (*) represents a nucleotide deletion. The complete sequence amplified in chinook salmon by the primers S-phe and P2 is given in Nielsen et al. (1994a).

Table 7

The numbers of fish (% in parentheses) found in five variable mtDNA haplotypes in populations of chinook salmon from New Zealand and the Sacramento River.

Population	*n*	mtDNA haplotype				
		1 and 4	2	3	5	6
Winter-run (CA)	72	70 (97)	0	0	0	2 (3)
Fall-run (CA)	359	233 (65)	14 (4)	35 (10)	77 (21)	0
Spring-run (CA)	59	35 (59)	0	16 (27)	8 (14)	0
CA total	490	338 (69.0)	14 (2.9)	51 (10.4)	85 (17.3)	2 (0.4)
Clutha (NZ)	62	51 (82)	0	0	11 (18)	0
Waitaki (NZ)	34	26 (76)	0	1 (3)	7 (21)	0
Rakaia (NZ)	37	30 (81)	0	6 (16)	1 (3)	0
Waimakariri (NZ)	39	34 (87)	1 (3)	1 (3)	3 (8)	0
NZ total	172	141 (82.0)	1 (0.6)	8 (4.7)	22 (12.8)	0

1994; Quinn and Foote, 1994) and may have reduced the effective population size further.

Ancestral population of New Zealand chinook salmon

Although the genetic and historical data clearly point to a seeding of NZ chinook from a Sacramento River population, identification of the specific ancestral population remains difficult. In addition to possible genetic changes in NZ chinook salmon over the years, the California populations have also undergone complex changes in abundance, habitat, and management since the turn of the century. Moreover, the seasonal runs are not monophyletic races but have apparently evolved independently in suitable habitats; hence major ancestral groups are generally based more on geography than on the timing of a run (Utter et al., 1993).

Aside from confirming a Sacramento River origin, the allozyme data provided no clues about the ancestral population. Both the absence of distinct alleles or of distinguishing frequencies of common alleles among contemporary temporal segments within the Sacramento River and the high genetic drift associated with the presumed bottlenecking in NZ precluded resolution from these nuclear variants. The mtDNA D-loop data, which theoretically provide higher resolving capabilities owing to higher mutation rates and greater population divergence of the haploid genome (Brown et al., 1982; Hoelzel et al., 1991), gave some clues but no definitive answers about the ancestral population (Table 7). The rate of molecular base changes at any one locus can vary according to the number and size of colonies, migration rates, sex ratios, type of parental transmission, as well as the expected rate of genetic drift (Birky et al., 1989; Martin and Palumbi, 1993). The haplotype profile of the Sacramento River fall-run fish resembled that of the combined NZ fish, sharing four haplotypes (1 and 4, 2, 3, 5). In contrast, the winter-run fish were the most distinct, lacking haplotypes 2, 3, and 5, and were represented by a unique haplotype 6 in two individuals. The spring-run sample contained haplotype 3 at a significantly higher frequency than that found for any NZ populations but shared a similar frequency profile for haplotype 5 with the combined NZ sample.

The genetic signatures of the spawning runs of chinook salmon found in the Sacramento River have probably changed since the transfers to NZ at the turn of the century owing to population bottlenecks (particularly the winter-run), hatchery manipulation, impacts from fisheries, changes in habitat, and changes in the thermal regime leading to overlap in temporal spawning populations. Prior to development of the Sacramento River system, Battle Creek had fall and spring runs of chinook salmon, and the current populations in the hatchery may have introgressed to some extent or been altered by interchange with chinook from other populations, despite efforts to maintain the runs separately. Cope and Slater (1957) noted that changes in the river's temperature regime delayed the arrival of spring-run fish at Battle Creek and that "This behavior, together with the fact that these two runs were forced to spawn on the same riffles, with the blocking of the river at Keswick Dam, is presumed to have brought about some mixing of the two stocks . . . when their spawning periods overlap in September. . . . At the hatchery . . . the dividing point between the spawning seasons of the two runs has been more or less arbitrarily set at September 25." Contemporary chinook salmon runs are defined by the timing of adult migration up the Sacramento River (Healey, 1991; Fisher[8]): fall-run (September–October), winter-run (November–February), and spring-run (March–May). These runs also differ in their spawning periods: fall-run (October–December), winter-run (May–June), and spring-run (August–September). Currently, there is also a putative "late fall-run," spawning in winter; unsampled in this study, these fish differed marginally from the fall-run in haplotype frequencies (Nielsen et al., 1994b). According to temporal criteria, the type of chinook embryos sent to NZ at the turn of the century were probably fall-run fish because Thomson (1922) reported that the shipments from California arrived ". . . early in January." Both the spawning season of the winter-run populations (late spring to early summer) and their mtDNA haplotype distribution indicate that they did not found the NZ chinook runs.

Some of the allozyme data raise additional questions about the ancestral population. Allelic variants at two loci occurred in two of the three NZ collections that were either rare (*HAGH*65*) or did not occur in any Sacramento River fish (*GR*110*). The occurrence of both of these variants in two populations (Rakaia and Waimakariri) and at frequencies as high as 0.135 (*HAGH*65*) minimizes the possibility of mutation after colonization. More likely, the variants were present in the founder population. If so, these alleles have drifted to a very low frequency or out of the sampled California populations or they were present in unusually high proportions in the founder population in NZ or in the two rivers in particular.

[8] Fisher, F. 1995. Calif. Dep. Fish and Game, Red Bluff, CA. Personal commun.

Interpopulation differences in NZ chinook

The reduced divergence among the three NZ populations indicated by the allozyme data, relative to the Sacramento River populations, may reflect the recent origins of the NZ groups. The similar magnitude of divergence evident among the NZ populations and between years within two Sacramento River fall-run hatchery populations (Fig. 3B) suggested no differentiation beyond year-class variation of a single population. The frequency of mtDNA types among the NZ stocks also did not indicate isolation between most populations. However, Clutha River fish (which expressed only two of the five haplotypes found in NZ samples) tended to be the most different, especially from Rakaia River fish. The Clutha River population, for which we had no allozyme data, was planted from the Hakataramea River in 1917 (McDowall, 1994) but has been landlocked since 1956 by Roxburgh Dam and may have undergone a population bottleneck after completion of the dam. The Clutha River population is thus less susceptible to genetic exchange than the three anadromous populations sampled, likely to be less polymorphic, and hence is not typical of NZ chinook.

The gene-frequency differences among the anadromous populations are consistent with panmixia caused by straying or successful transfers of salmon among the rivers. Unwin and Quinn (1993) documented straying rates of about 12% by hatchery-released chinook salmon from the Rakaia River to other NZ rivers. In addition, during the 1980's several million juvenile salmon were transferred from the Rakaia, Rangitata, and Waimakariri Rivers to virtually all major east coast rivers except the Rakaia River. Nevertheless, the populations now differ in many life history traits, including fecundity (Quinn and Bloomberg, 1992), freshwater and marine age, length at age, weight at length, date of return to freshwater, and spawning date (Quinn and Unwin, 1993), and egg size and body shape.[9] These phenotypic differences are consistent with some level of genetic isolation among the populations but do not demonstrate it (Waples, 1995).

Our results provide a perspective on the management and conservation of salmon populations. Founder effects or strong selection against certain genotypes can reduce the genetic diversity of populations established by colonization, relative to the source population. However, the NZ experience indicates that this may not prevent the transplant from being successful. The life history differences among NZ populations indicate that salmon populations may evolve quite quickly, although the genetic basis of the life history differences seen in NZ has yet to be demonstrated. The implications of such rapid evolution are open to interpretation. One might argue that it demonstrates the importance of the stock concept in salmon management because reduced gene flow and population adaptation are such fundamental aspects of salmon biology. One might be encouraged to attempt to restore salmon populations to areas from which they have been extirpated, given a suitable source population. However, skeptics of the application of the species concept (including the U.S. Endangered Species Act) to salmon populations might argue that the rapid diversification of salmon populations indicates that they are more plastic than has been assumed and that only a diverse gene pool needs be preserved, not every spatially and genetically discrete population. The concept of "evolutionarily significant unit" (Waples, 1995) provides a compromise by focusing on critical genetic and ecological variables involved in grouping and managing populations. In any case, it is important to remember that the success of the NZ chinook transplant was the exception and that the vast majority of other transplants have failed. Presumably, local adaptation was not sufficiently rapid or flexible to prevent extinction.

[9] Unwin, M. J., M. Kinnison, N. Boustead, and T. P. Quinn. In prep. Variation in body size and morphology of adult chinook salmon (*Oncorhynchus tshawytscha*) from two New Zealand populations and their ancestral Sacramento River, California, population, ninety years later. Natl. Inst. of Water and Atmosphere, P.O. Box 8602, Christchurch, New Zealand.

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Seasonal abundance, growth, and foraging habits of juvenile smooth dogfish, *Mustelus canis*, in a New Jersey estuary*

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Abstract.—Smooth dogfish, *Mustelus canis*, were collected with weirs, seines, gill nets, trawls, and by hook and line from 1988 to 1990 in the Little Egg Harbor–Great Bay estuary of southern New Jersey to determine their foraging habits, growth, and seasonal, tidal, and diel patterns of abundance. Young of the year (YOY) were collected from May to October, with apparently newborn individuals dominating catches from May to July. Subadult and adult individuals were rare. Young of the year reached 550–700 mm total length (TL) by October, growing an estimated 1.9 mm TL/day and 6.0 g/day. Tidal and diel patterns suggest that smooth dogfish use shallow shoal and marsh creek habitats primarily during night hours. High catches during flood tides also suggest increased activity at that time. A comparison of abundance patterns among gears suggests that marsh creeks may be particularly important to newborn individuals during June–July. From an analysis of sex ratio patterns, young of the year do not appear to aggregate by sex or exhibit different emigration patterns between sexes. Smooth dogfish YOY feed primarily on small shrimps, *Crangon septemspinosa* and *Palaemonetes vulgaris*, polychaete worms, and the crabs *Callinectes sapidus, Libinia* sp., and *Ovalipes ocellatus*. The abundance of YOY within the estuary strongly suggests that estuaries are critically important nursery habitats for smooth dogfish within the Mid-Atlantic Bight.

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The smooth dogfish, *Mustelus canis*, is one of the most abundant inshore sharks in the western Atlantic (Smith, 1907; Bigelow and Schroeder, 1948, 1953; Hoese, 1962; Compagno, 1984). Despite its abundance, little ecological information, other than anecdotal accounts of growth, and seasonal and life history patterns, is available (Castro, 1983; Compagno, 1984). The most comprehensive accounts of smooth dogfish are found in two summaries by Bigelow and Schroeder (1948, 1953); however, little data on distribution, length frequency, or reproduction are presented in these general descriptive accounts. Food habits have been examined by Field (1907) and Breder (1921). Several studies have examined physical aspects of reproduction (Fowler, 1918; TeWinkel, 1950, 1963, 1964; Graham, 1967; Gilbert and Heath, 1972; Hisaw and Abramowitz[1]), other physiology and behavior (Parker, 1909, 1913; Ifft and Zinn, 1948; Clark, 1963; Gilbert, 1963) and growth (Moss, 1972; Francis, 1981). Although a small fishery for smooth dogfish has grown in recent years, with landings in excess of 780,000 lb and valued at over $100,000 during 1992,[2] the greatest value in smooth dogfish has probably been its extensive use as a subject for research in medical physiology, morphology, and molecular biology (e.g. Greig, 1977; Kalmijn, 1977; Hodgson and Mathewson, 1978; Casterlin and Reynolds, 1979, a and b; Bartlett, 1982; Barry et al., 1988).

In this study we examine aspects of smooth dogfish habitat during that part of the first year of life when estuaries are used as nurseries. More specifically, we collect data with a variety of gears within an estuary of southern New Jersey to determine seasonal abundance and habitat use patterns, growth, and food habits of smooth dogfish.

* Contribution 96-12 from the Institute of Marine and Coastal Sciences, Rutgers University, New Brunswick, New Jersey 08903.

[1] Hisaw, F. L., and A. A. Abramowitz. 1937. The physiology of reproduction in the dogfish, *Mustelus canis*. Annual Rep., Woods Hole Oceanogr. Inst. 1937: 21–22.

[2] Fishery Analysis Div., Fisheries Information Section, National Marine Fisheries Service, Gloucester, MA.

Materials and methods

Study area

The study was conducted in polyhaline (22–33‰) sections of the Little Egg Harbor–Great Bay estuary in southern New Jersey during 1988–90 (Fig. 1). Primary sampling was conducted within tidal marsh creek and adjacent bay shoal habitats with several gear types (Table 1). The four primary study creeks (Schooner, New, Foxboro, and Story Island creeks) were approximately 1.0 km long blind cul-de-sacs that received fresh water only through local runoff (Fig. 1). Story Island Creek was intertidal except for a shallow (<0.5 m) subtidal cove formed at the mouth at low tide. The other three creeks were subtidal with maximum depths of 0.5–2.0 m at low tide. All creeks had a mud substrate and were located 1.3–2.9 km from Little Egg Inlet (for a more complete description of the study creeks see Rountree [1992]). The marsh creeks are typically separated from the adjacent bay by a shallow sill formed at the creek mouth. Beyond the sill, Story Island and Foxboro creeks emptied onto extensive bay shoals (<2 m at high tide) bordering the relatively deep (4–9 m at high tide) Marshelder Channel (Fig. 1). In contrast, New and Schooner creeks each emptied directly into deep channels (Fig. 1).

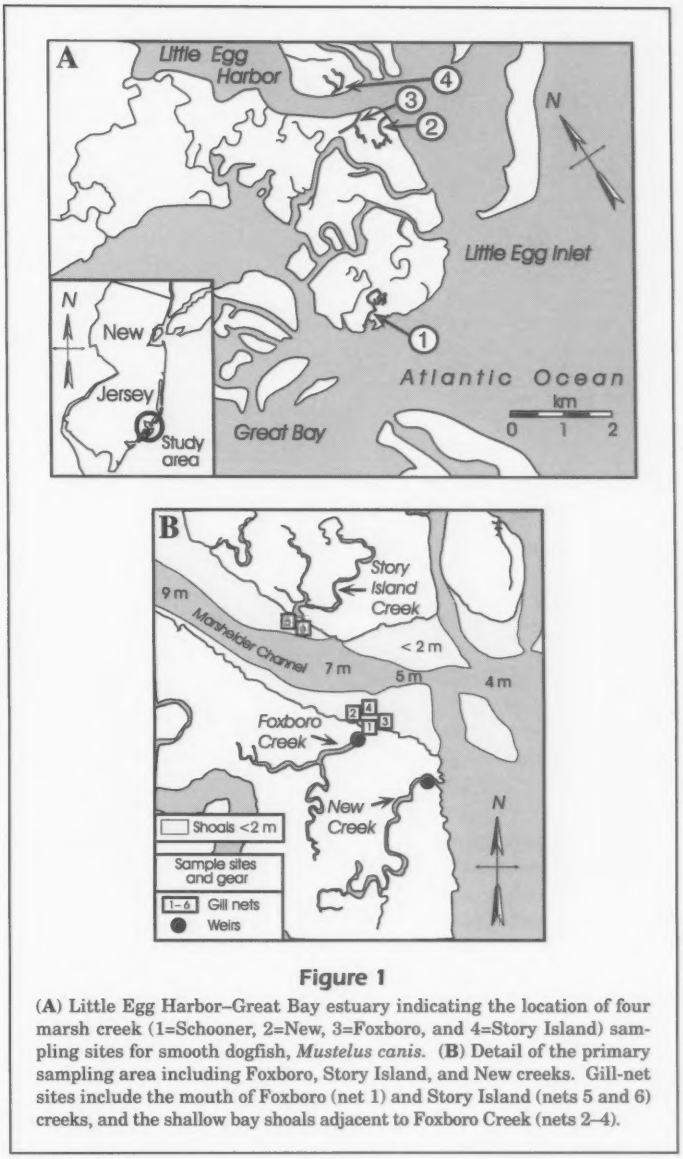

Figure 1

(**A**) Little Egg Harbor–Great Bay estuary indicating the location of four marsh creek (1=Schooner, 2=New, 3=Foxboro, and 4=Story Island) sampling sites for smooth dogfish, *Mustelus canis*. (**B**) Detail of the primary sampling area including Foxboro, Story Island, and New creeks. Gill-net sites include the mouth of Foxboro (net 1) and Story Island (nets 5 and 6) creeks, and the shallow bay shoals adjacent to Foxboro Creek (nets 2–4).

Sampling techniques

The creeks were sampled with weirs, seines, and gill nets (Table 1). Shallow bay shoal habitats adjacent to Foxboro and Story Island creeks were sampled with gill nets and hook and line (Fig. 1). Additional data were derived from extensive trawl collections made in many habitats throughout the estuary, including other marsh creeks and Marshelder Channel in the vicinity of Foxboro Creek (Szedlmayer et al., 1992; Szedlmayer and Able, in press).

Weir and seine sampling For each sampling event, a temporary weir was erected at high tide approximately 30 m above the creek sill. The creek was blocked off entirely by two wing nets (15.2 m × 3.0 m; 6.4-mm mesh) that ran at an angle from each creek bank to a weir (1.2 m wide × 3.0 m long × 3.0 m high; 6.4-mm mesh) located in the center of the creek channel. Deployment of the weir and wings began about 30 min before slack high tide and was completed within 1 h. Fish moving out of the creek with the ebb tide were led along the wings into the weir, where they were trapped by two sets of internal doors. Live fish were removed from the weir at low tide through a codend after raising the weir above the water line. The weir was removed from the creek after each sampling event.

In an effort to capture fish that did not move into the weir during the ebb tide, seine samples were taken at low tide (immediately prior to hauling the weir) within the approximately 100-m^2 triangular area enclosed by the wings. See Rountree and Able (1992) for a more complete description of the weir and seine sampling methods.

Intensive weir and seine sampling was conducted approximately fortnightly from April to November 1988 in Schooner and Foxboro creeks and from April to October 1989 in Schooner, Foxboro, and New creeks (Table 1). During 1988, consecutive day and night tides were sampled within each creek, whereas only night tides were sampled during 1989. Day and night tides were those in which at least the last two hours of flood occurred after sunrise or sunset, respectively. During 1988 and 1989 all creeks were sampled within a three-d period during each sampling week.

Gill-net sampling Standardized gill-net sampling at fortnightly intervals was conducted during May and July–November 1990 with six gill nets (23 m long × 1.8 m high; 38-mm^2 mesh; Table 1). One net was set on the sill at the mouth of Foxboro Creek, and three were set in the shallow bay shoals adjacent to the creek. Two additional nets were set in the mouth of Story Island Creek (Fig. 1). The first gill net was stretched across the mouth of Foxboro Creek so as to block fish passage completely. However, at Story Island Creek two nets were stretched across the creek mouth but did not completely block the creek entrance. Gill nets were deployed at night between 1600–2200 h at either high or low tide and were checked 2–6 times until 0900–1100 h the next day. Catches of smooth dogfish were standardized by catch per unit of effort (CPUE) which was determined "as the number of fish captured in a net check divided by the time elapsed since the previous check (expressed as number/net hours)." Sampling effort was similar on ebb and flood tides (298 and 252 net h, respectively; Table 1). These data were supplemented with data from irregular gill-net collections made on four dates during 1988 and on two dates during 1989 within either Foxboro or Schooner creeks (Table 1).

Other sampling Irregular collections with hook and line were made in the immediate vicinity of Foxboro Creek, although some collections were made in other areas of the bay (Table 1), and standardized otter-trawl tows (4.9-m opening, 19-mm-mesh wings, 6.3-mm-mesh liner) were made during the day at 13 locations throughout the Little Egg Harbor–Great Bay

Table 1

Sampling effort and size ranges of smooth dogfish, *Mustelus canis*, collected in the Little Egg Harbor–Great Bay estuary of southern New Jersey during 1988–90.

				Young-of-the-year total length (mm)				Other total length (mm)			
Gear	Year	Sampling period	Sampling effort	Mean (SE)	Min	Max	*n*	Mean (SE)	Min	Max	*n*
Weir	1988	Apr–Nov, fortnightly (day and night)	42 sets	421 (5)	285	539	68	— (—)	—	—	—
	1989	Apr–Oct, fortnightly (night)	27 sets	388 (9)	299	545	37	627 (—)	627	627	1
Seine	1988	Jul–Nov, fortnightly (day and night)	32 hauls	422 (7)	369	453	12	— (—)	—	—	—
	1989	Apr–Oct, fortnightly (night)	25 hauls	387 (29)	320	481	6	— (—)	—	—	—
Gill net	1988	Jun–Sep (irregular)		400 (11)	318	462	14	945 (131)	728	1,180	3
	1989	Aug–Sep (night)	138 h[1]	499 (12)	366	604	22	— (—)	—	—	—
	1990	May, Jul–Nov, fortnightly (night)	550 h	520 (3)	389	699	448	825 (68)	592	1,025	8
Hook-and-line	1988	Jun–July (day and night)	2 dates	473 (11)	418	515	9	1,123 (39)	1,070	1,200	3
	1989	Jun–Sep, irregular (day and night)	5 dates	380 (6)	321	517	48	— (—)	—	—	—
	1990	May–Jun, irregular (day and night)	7 dates	397 (7)	325	460	33	996 (158)	715	1,260	3
Otter trawl	1988	June–Dec, monthly (day)	342 tows	429 (9)	380	472	11	1,156 (11)	1,126	1,220	7
	1989	Jan, Mar–Jun, Sep–Oct, monthly									
		Jul–Aug, fortnightly (day)	563 tows	419 (19)	371	522	7	— (—)	—	—	—
	1990	Apr–Dec, monthly (day)	560 tows	355 (11)	326	379	5	— (—)	—	—	—

[1] Total number of hours fished summed over all nets.

estuary (Table 1). Four replicate 2-min tows were made at each location. One of the trawl stations was located in Marshelder Channel in the vicinity of Foxboro and Story Island creeks. Trawl samples were collected monthly, except for fortnightly sampling during July, August and September 1989 and 1990 (Szedlmayer et al., 1992; Szedlmayer and Able, in press).

Sex ratio patterns

The sex ratio (percent female and male) was determined for each net check in which at least three fish were collected. The sex ratio of smooth dogfish observed at each net check was used as a proxy for the sex ratio of smooth dogfish schools. If this assumption is valid, then significant deviations from equal proportions would suggest that schools segregate by sex. We also tested for temporal changes in sex ratio, which would suggest differential timing of seasonal movements by sex. Deviations from expected ratios were tested by chi-square analysis (SAS Institute, Inc., 1988).

Growth rate

Temporal trends, and differences between sexes in absolute growth rates were estimated by linear regression of fish size on date of capture. Length outliers from each sampling period, which were assumed to represent age-1 or older individuals from an examination of length-frequency distributions (Table 1; Fig. 2), were removed prior to the regression. An-

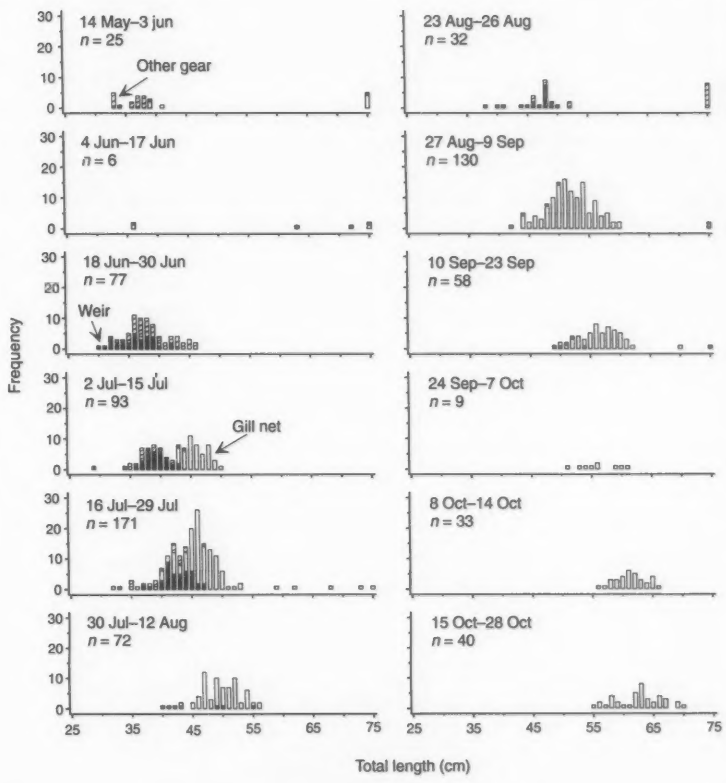

Figure 2

Total length (TL) frequency distribution of smooth dogfish over fortnightly sampling periods, based on data pooled over all years (1988–90) and sampling gears (weir, seine, hook and line, otter trawl, and gill net). Solid bars indicate weir or seine samples, open bars indicate gill-net samples, and striped bars indicate combined hook-and-line and otter-trawl samples. All individuals >75 cm TL are lumped into the 75-cm size class.

nual and sex-stage effects on growth rates were tested with an Analysis of Covariance (ANCOVA) with the following model:

$$\text{Length} = \text{Year Sex Year*Sex Date Year*Date Sex*Date Year*Sex*Date},$$

with the SAS GLM procedure (Freund et al., 1986; SAS Institute Inc., 1988), where year and sex are class variables and date is a covariate. The test of the main effects (year and sex) represents a test for differences in y-intercepts, whereas the test of the interaction with the covariate represents a test for heterogeneity of slopes (Freund et al., 1986). Growth in terms of body weight was similarly tested.

Habitat use patterns

A statistical comparison of smooth dogfish abundances among marsh creeks was made by using an ANOVA, based on night-time weir sampling in Foxboro, Schooner, and New creeks conducted during 1989. We previously reported a comparison between day and night abundances of smooth dogfish in Foxboro and Schooner creek sampling during 1988 as part of a study of diel variation in marsh creek faunal composition (Rountree and Able, 1993). Descriptive statistics, based on night-time gill-net sampling in 1990, were used to compare catches between marsh creek and adjacent bay shoal habitats as well as between ebb- and flood-tide stages. Because time of day, tide stage, and seasonal effects could not be partitioned in the 1990 gill-net sampling, no attempts were made to statistically test hypotheses of habitat or tide stage differences in catches. For example, gill-net sampling was biased between habitats because nets stretched across creek mouths were presumably more efficient than those placed in the open bay. Additionally, because tide and diel cycles are not correlated, sampling on flood and ebb tides were sometimes conducted weeks apart (i.e. it was impossible to sample on both flood and ebb tides at the same location and time).

Foraging habits

Smooth dogfish collected in 1988–90 during gill-net, hook-and-line, and trawl sampling were measured live, packed in ice, and transported to the laboratory for freezing. Because of the large number of smooth dogfish captured during 1990 gill-net sampling, a subsample of at least three fish was retained from each net check for food habit analysis. The remaining fish were tagged and released. The released fish were tagged to prevent bias in the catch estimated from recaptures. Fish were tagged just posterior to the first dorsal fin with individually coded yellow T-bar anchor tags (total tag length, 40 mm; Hallprint Pty. Ltd., Holden Hill, South Australia). Because no tagged individuals were recovered during our gill-net sampling, CPUE adjustments were not necessary.

In the laboratory, thawed smooth dogfish were remeasured and weighed prior to stomach removal. The total stomach contents were then weighed and the prey items were identified to the nearest taxon, enumerated, and weighed (wet WT). An index of gut fullness (%full) that incorporates body weight rather than gut capacity (Hyslop, 1980) was calculated as

$$\%full = [(prey\ WT)/(total\ body\ WT - total\ gut\ WT)] \times 100,$$

where *prey WT* = the weight of a given prey species (or sum of all prey species);
total body WT = the total weight of the smooth dogfish; and
total gut WT = the weight of the entire gut contents (excluding the stomach itself).

Tidal and temporal (hour of the night) effects on stomach, large intestine, small intestine, and total digestive tract fullness were examined from 1990 gill-net samples. After having been thawed in the laboratory, the entire digestive tract was excised and sectioned into stomach, large intestine (spiral valve), and small intestine (colon and rectum). The total contents of each section, as well as the total for all sections combined, were then weighed. After pooling data from all collections for each tide stage, hourly mean fullness values were calculated for each gut section separately, as well as for the total. The effect of tide stage (ebb vs. flood) on gut fullness indices was tested separately for each section of the digestive tract and for the total digestive tract, with analysis of variance (ANOVA; Sokal and Rohlf, 1981). Use of the fullness index, described above, allowed us to reduce bias due to variation in dogfish size in the ANOVA. The data were arcsine–square-root transformed prior to analysis.

Results

Life history stages and seasonal abundance patterns

Most smooth dogfish collected in the study area were YOY according to size at date of capture (Fig. 2) and according to an assumed length of 80–90 cm at ma-

turity (Castro, 1983; Compagno, 1984). A total of 720 YOY and 25 subadult (60–80 cm) to adult (80–130 cm TL) smooth dogfish were collected (Table 1). A single well-defined size cohort of YOY dominated catches on the basis of data pooled over all years and gears (Table 1; Fig. 2). The smallest individuals (<40 cm) collected during May, June, and early July had fresh umbilical scars. Although adults were not abundant, they were collected from May to September. Their relative rarity, however, may have been due to gear avoidance, because we frequently observed adults during night flood tides in the shallow bay in the vicinity of Foxboro and Story Island creeks from May to July. Additionally, on several occasions we observed adults that repeatedly came into contact with gill nets without becoming entangled. A few intermediate-size individuals (60–70 cm TL) were collected in June, July, and September. These individuals appeared to be small subadults from their length at date of capture (more strikingly, they were far more robust than the YOY and lacked umbilical scars) and were excluded from the growth analysis for the YOY.

The occurrence of YOY in the study area was highly seasonal. They appeared first in May and apparently left the study area by November (Figs. 3 and 4). The timing of fall migration out of the estuary was well defined by their absence in weir, gill-net, and trawl samples during November. The first appearance of YOY during the spring, however, was less well defined because of the lack of gill-net sampling during this period, despite their absence in April weir and seine sampling as well as January–April trawl sampling. Young of the year were abundant in weir and seine collections only during June and July (Fig. 3).

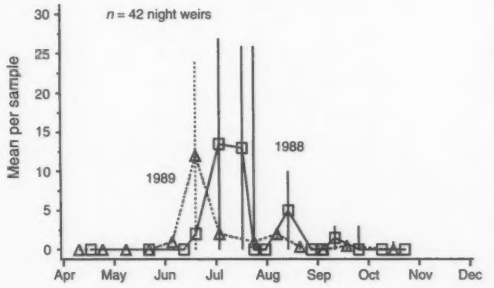

Figure 3

Seasonal abundance of smooth dogfish, based on night weir samples pooled from three subtidal marsh creeks (Foxboro, New and Schooner) during 1988 and 1989 (vertical lines represent one standard error about the mean). Smooth dogfish were absent from day weir samples.

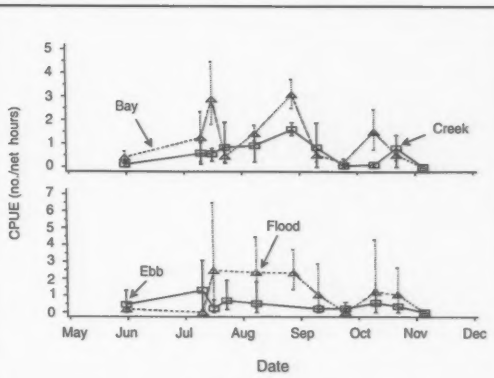

Figure 4

Seasonal abundance (CPUE expressed as the mean number per hour per net) of smooth dogfish collected with gill nets set in marsh creeks and in the adjacent shallow bay during 1990. Data are grouped by habitat (top) and tide stage (bottom) for comparison. Vertical lines are ranges.

In contrast, they were collected regularly in gill-net samples from both the bay shoal and marsh creek sill locations from June through October (Fig. 4). Peak CPUE in gill-net sampling occurred from July to August. Young of the year collected by weir tended to be smaller than those collected by other gears during June–August (Fig. 2). No tagged (n=138) YOY were recaptured during our sampling; however, two individuals were recaptured off North Carolina the following winter: one inshore near Cape Fear, North Carolina, in December 1990 and a second off the beach at Cape Hatteras, North Carolina, in March 1991.

Sex ratio

Sex ratios of the YOY did not differ significantly from 1:1, averaging 51.8 % (standard error [SE]=2.8) females per net check (n=55 net checks with three or more fish). No significant temporal effect on sex ratio was observed.

Growth

Young of the year exhibited a very rapid growth rate of 1.9 mm TL/day, or 6.0 g/day (Table 2), and reached 550–700 mm TL by the end of October (Fig. 2). There was a significant annual affect on growth rates for both length and weight (i.e. the slopes were not homogeneous among years; ANCOVA, $P \leq 0.0001$; Table 2; Fig. 5). No effect of sex on growth was observed (Table 2; Fig. 5). Because the slopes were heterogeneous among years, differences in intercepts among years could not be tested; however, a significant dif-

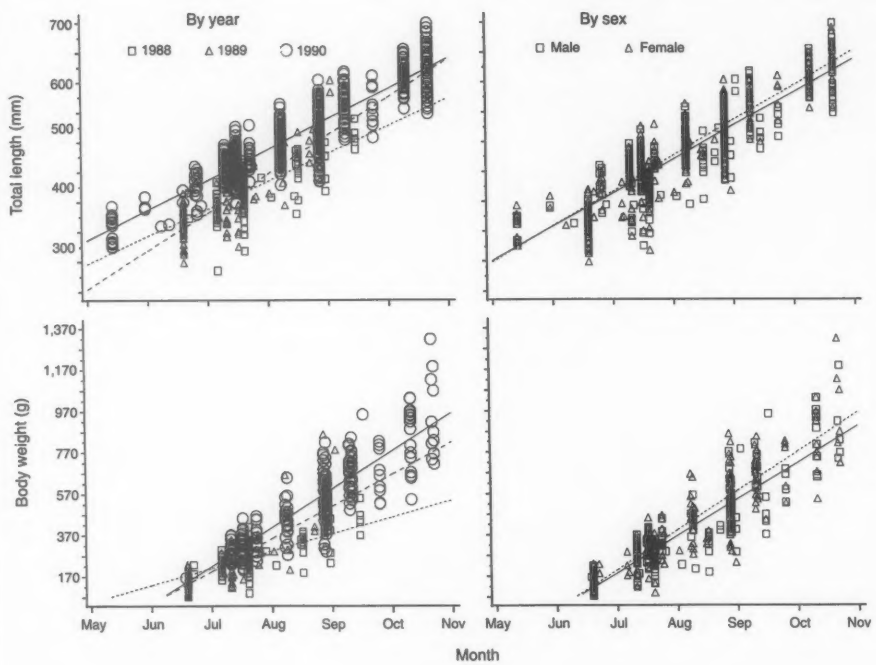

Figure 5

Comparison of total length (TL) and body weight (WT) growth rates of smooth dogfish by sampling year and sex. Linear regression parameter estimates and statistics are given in Table 2.

Table 2

Growth rates of young-of-the-year smooth dogfish collected from the Little Egg Harbor–Great Bay estuary of southern New Jersey between 1988 and 1990, estimated by linear regression of total length and body weights on dates of capture. All parameter statistics are significant at $P \leq 0.0001$.

	Length (mm TL/d)			Weight (g/d)		
	Slope (SE)	r^2	n	Slope (SE)	r^2	n
Year[1]						
1988	1.51 (0.14)	0.50	114	2.70 (0.28)	0.47	103
1989	2.09 (0.11)	0.74	120	5.08 (0.31)	0.73	101
1990	1.66 (0.04)	0.82	486	6.04 (0.24)	0.76	208
Sex[2]						
Male	1.84 (0.05)	0.78	345	5.78 (0.22)	0.80	181
Female	1.93 (0.05)	0.79	329	6.20 (0.23)	0.78	196
Pooled	1.91 (0.04)	0.78	720	6.01 (0.15)	0.79	412

[1] Growth rates are highly significantly different among years (ANCOVA, $P \leq 0.0001$) for length and weight.
[2] Samples sizes are lower because sex was not determined for some individuals during 1988. Growth rates are not significantly different between sexes.

ference in the y-intercepts between sexes was observed for weight (ANCOVA, $P \leq 0.001$; Fig. 5), suggesting that females may have been born slightly heavier (approx. 42 g) than males. A highly significant length-weight relationship was obtained (Fig. 6). No differences in the length-weight relationship were found between sexes.

Habitat use patterns

Habitat type (tidal creek versus adjacent bay shoals), time of night, and tide stage (ebb versus flood) had a strong effect on CPUE of smooth dogfish in gill-net collections (Figs. 4 and 7). Most smooth dogfish were captured on flood tides (Fig. 4), with flood tide CPUE averaging 1.1 fish/net h (SE=0.2), and ebb tide CPUE averaging 0.5 fish/net h (SE=0.1). Catches were greatest at 2100 h (3 fish/net h) and declined sharply by 0300 h (<0.6 fish/net h), and dropped to near zero by 0600 h (Fig. 7). Catches tended to be greater in the bay shoal habitat than at the creek sills (Fig. 4), with CPUE averaging 1.2 fish/net h (SE=0.2) and 0.6 fish/net h (SE=0.1), respectively. Abundance of YOY in weir samples varied significantly ($P \leq 0.5$) among Foxboro, Schooner, and New creeks, averaging 3.7, 0.3, and 0.8 individuals/weir, respectively.

Foraging habits

Dominant prey of YOY smooth dogfish included the shrimps *Crangon septemspinosa* and *Palaemonetes vulgaris*, polychaetes, and the crabs *Callinectes sapidus*, *Libinia* spp., and *Ovalipes ocellatus* (Table 3). The diet of YOY included several other small decapod crabs, razor clam *(Ensis directus)*, and small fishes (*Menidia menidia* and *Fundulus heteroclitus*). Often, YOY dogfish stomachs contained the walking legs or chelae of crabs, rather than entire individuals. Soft shell individuals of the various crab species were also frequently consumed. Whole crabs, other than those recently molted, were rarely observed.

There were no strong tidal or hourly trends in gut fullness (Fig. 8). No empty stomachs were found. Stomach fullness averaged 5.04 % body wt (SE=0.21, n=136), and 4.21 % body wt (SE=0.21, n=107) for individuals captured during flood and ebb tides, respectively. Stomach fullness increased slightly from early evening (averaging about 4 % body wt at 1900 h) to early morning (averaging about 5 % body wt at 0600 h). Three fish examined during mid-afternoon also had high levels of food in their stomachs (4–6 % body wt at 1200–1300 h). Intestine fullness remained remarkably constant regardless of time of night (hourly means ranging from 0.4–0.5% body wt, and 1.5–1.9 % body wt for the small and large intestine, respectively). We did not observe any strong decline in stomach fullness or any increase in intestinal fullness that would suggest noncontinuous feeding.

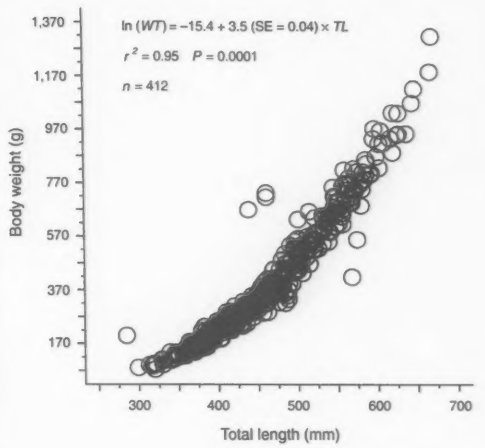

Figure 6

Total length (TL)-body weight (WT) relationship for smooth dogfish based on data pooled over all years and gears (n=412, r^2=0.96, $P \leq 0.0001$).

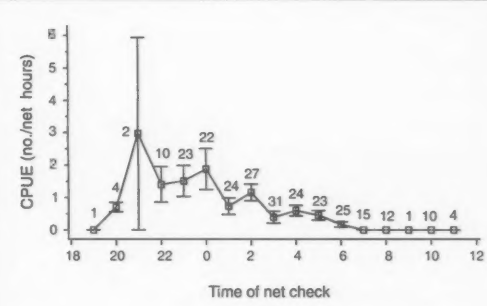

Figure 7

Hourly mean abundance (CPUE per hour per net) of smooth dogfish collected during the night with gill nets set in marsh creeks and adjacent bay habitats during 1990. Data are grouped by ebb- and flood-tide stage. Vertical lines are ranges.

Discussion

Life history stages and seasonal abundance patterns

Smooth dogfish are seasonal residents in New Jersey estuaries; adults are present April–September,

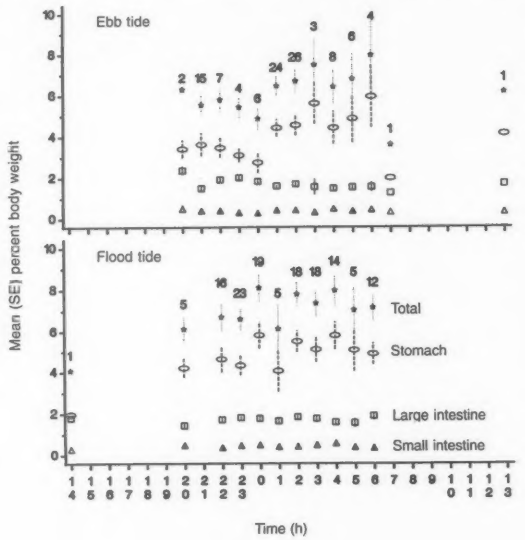

Figure 8

Hourly change in total digestive tract, stomach, large intestine, and small intestine fullness expressed as mean percent of body weight for smooth dogfish caught during ebb (top) or flood tide (bottom). Vertical bars are ranges in percent of body weight for individual fish. Numbers above symbols indicate the number of stomachs sampled during that hour.

and YOY are present May–October (Figs. 2–4). Most adults, however, appear to leave the estuary by mid-July (Rountree, personal observ.). The rarity of adult individuals in our samples results partly because they avoid gear and partly because they do not appear to use the shallow creeks and thus were not captured in weir sampling. However, adults were frequently observed in the bay and are often caught by local fishermen during late spring–early summer (Rountree, personal observ.). The near absence of subadults, however, in our collections may reflect a true rarity in the estuary.

The coincidental arrival of both mature adults and newborn YOY to Mid-Atlantic Bight estuaries suggests that adults use estuaries as a parturition ground. However, we did not observe any evidence of parturition within the estuary during our study, other than the capture of YOY presumably only days old (Rountree, personal observ.). It is not known whether parturition actually occurs in the estuaries or in inshore marine waters (surf zone to inner shelf) or in both. Uncertainty of the importance of estuaries as parturition habitats is underscored by the fact that the use of estuaries and coastal waters is characteristic only for the northern Atlantic population. The same species may only inhabit deeper shelf waters in other areas (Bigelow and Schroeder, 1948; Baughman and Springer, 1950; Hildebrand, 1953).

The size of smooth dogfish at birth has been widely reported as 34–39 cm (Bigelow and Schroeder, 1948; Hildebrand, 1953; Heemstra, 1973; Castro, 1983; Compagno, 1984), despite the fact that Bigelow and Schroeder (1953) later reported size at parturition to be 29–37 cm TL (11.5–14.5 inches). Because we collected post parturition individuals as small as 28 cm TL (Fig. 2), we suggest that a range of 28–39 cm TL at parturition is more accurate. However, we know of no published data on size at parturition, other than anecdotal accounts (Field, 1907; Smith, 1907; Fowler, 1918; Baughman and Springer, 1950; Hildebrand, 1953; Graham, 1967). Until length-frequency data of full-term embryos can be compared with length-frequency data for post parturition YOY, our estimate of 28–39 cm at birth should be used cautiously. Assuming this estimate is correct, we conclude from the size distribution of YOY that parturition of YOY in New Jersey waters occurs from mid-May through July (Figs. 2 and 5). Similar periods of parturition

Table 3

Food habits of 85 young-of-the-year smooth dogfish (mean, 417 mm; range 318–586 mm TL) collected in Little Egg Harbor–Great Bay estuary with gill net, trawl, and hook and line from April to November 1988–90. Percent frequency of prey among stomachs, mean number and weight of prey per stomach, and mean gut fullness index (100 × prey weight/body weight) are given for all prey occurring in at least 1% of the stomachs. The combined rank is a rank of the sum of the ranks for each measure. No stomachs were empty.

Prey species (or category)	Percent frequency	Mean (SE) number	Mean (SE) weight	Mean (SE) fullness	Combined rank
Crangon septemspinosa	65	1.41 (0.20)	0.32 (0.06)	0.21 (0.04)	1
Polychaete	47	0.48 (0.06)	0.17 (0.04)	0.09 (0.03)	5
Unidentified crabs	47	0.48 (0.06)	0.58 (0.13)	0.21 (0.04)	1
Palaemonetes vulgaris	32	1.34 (0.42)	0.54 (0.19)	0.25 (0.08)	3
Callinectes sapidus	12	0.22 (0.06)	0.86 (0.40)	0.27 (0.14)	4
Libinia sp.	9	0.12 (0.04)	0.53 (0.26)	0.14 (0.07)	6
Ovalipes ocellatus	9	0.12 (0.04)	0.22 (0.11)	0.06 (0.03)	7
Miscellaneous	8	0.09 (0.03)	0.04 (0.02)	0.01 (0.01)	11
Unidentified fish	8	0.09 (0.04)	0.07 (0.04)	0.02 (0.01)	8
Unidentified bivalve	7	0.08 (0.03)	0.02 (0.01)	0.01 (0.01)	14
Cancer sp.	5	0.09 (0.04)	0.06 (0.03)	0.02 (0.01)	10
Ensis directus	5	0.05 (0.02)	0.06 (0.03)	0.02 (0.01)	13
Upogebia affinis	2	0.06 (0.03)	0.13 (0.08)	0.04 (0.02)	9
Menidia menidia	2	0.02 (0.02)	0.12 (0.09)	0.04 (0.03)	12
Isopoda	1	0.04 (0.03)	<0.01	<0.01	16
Carcinus maenus	1	0.01 (0.01)	<0.01	<0.01	17
Neopanopeus sp.	1	0.01 (0.01)	<0.01	<0.01	17
Fundulus heteroclitus	1	0.01 (0.01)	0.10 (0.10)	0.04 (0.04)	15
Unidentified shrimps	1	0.01 (0.01)	<0.01	<0.01	17
Pagurus longicarpus	1	0.04 (0.04)	<0.01	<0.01	17
Total crabs	95	1.06 (0.11)	2.26 (0.48)	0.70 (0.16)	
Total shrimps	98	2.76 (0.46)	0.86 (0.20)	0.46 (0.09)	
Total other	89	0.96 (0.11)	0.73 (0.20)	0.29 (0.08)	
Total		4.79 (0.44)	3.85 (0.53)	1.46 (0.18)	

have been reported elsewhere (Bigelow and Schroeder, 1948, 1953; Graham, 1967; Castro, 1983; Compagno, 1984; Hisaw and Abramowitz[1]).

Growth rate

Our estimates of growth rates, based on length-frequency analysis, suggest that smooth dogfish YOY grow very fast during the nursery period (nearly 2 mm TL/day) and attain a size of 55–70 cm TL (mean=63 cm) by the time they leave the estuary in the fall. That such high growth rates are possible is confirmed by a single tag return (out of 17 fish tagged during 1989 weir sampling) in which a YOY male grew 44 mm in 24 days, averaging 1.8 mm TL/day. Similar growth-rate estimates have previously been reported. Hisaw and Abramowitz[1] suggested that smooth dogfish females grow about 20–30 cm per year, which corresponds to lengths of 48–70 cm TL by their first year. Moss (1972) later used tooth width and tooth replacement data to estimate a growth rate of 1.4–1.7 mm TL/day for the first year, which overlaps with our growth-rate estimates (Table 2). Extrapolation from the von Bertalanffy growth curve provided by Moss (1972) suggests that fish reach about 60 cm by the end of their first six months of life (roughly October). This estimate agrees well with our estimate. Moss's (1972) growth estimate also reveals no difference in growth between sexes during the first year, which agrees with our observations.

The significant annual differences in our growth rate estimates probably resulted from annual differ-

ences in the timing of peak abundance of YOY in the weir samples (Fig. 3) and to sampling bias among the gears. The bimodal length-frequency pattern observed in July (Fig. 2) was caused by the later occurrence of YOY during 1989 compared with 1988 (Fig. 3) and results in an increased slope of the regression of length on date for 1989 compared with 1988 and 1990. Bigelow and Schroeder (1953) and Graham (1967) also noted annual variation in peak abundance of YOY. The cause of this annual variation is not known at this time.

The statistically significant differences in the y-intercepts for weight between sexes is puzzling. If real, it suggests that females are larger at birth than males and, given that adult females tend to be larger than adult males (Bigelow and Schroeder, 1948; 1953; Castro, 1983; Compagno, 1984), that this size difference is maintained throughout life despite equal growth rates. However, data on actual size at birth are necessary to confirm this hypothesis.

Habitat use patterns

Smooth dogfish exhibit a strong nocturnal pattern in habitat use. We have previously reported from weir sampling that smooth dogfish appear to use subtidal marsh creeks exclusively during the night (Rountree and Able, 1993). In fact, no dogfish have been collected during the day in the creeks that we studied despite intensive sampling (Table 1). The hourly YOY CPUE pattern in the more recent gill-net sampling supports this observation (Fig. 7). Additionally, smooth dogfish are known to exhibit a nocturnal activity rhythm (Casterlin and Reynolds, 1979a). Also, individuals that were trapped in the creeks by the weir and its wings appeared to become increasingly stressed as low tide approached. Stressed individuals were often observed to thrash around with their heads out of the water. These patterns strongly suggest that YOY smooth dogfish undergo nocturnal tidal migrations in and out of the bay shoal and marsh creek habitats during the night.

Bay shoal habitats may be important YOY habitats within the estuary. Young of the year were very abundant within Foxboro and Story Island creeks, which bordered extensive shoal areas (Fig. 1), but were much less abundant at New Creek and Schooner Creek, which both empty directly into deep channels. Abundances in Foxboro Creek weir samples were significantly greater than in either Schooner or New creek. The low abundance in New Creek weir collections is particularly striking because YOY were abundant in Foxboro Creek despite it being located less than 300 m away. The importance of bay shoals adjacent to marsh creeks is supported by our observations (from informal gill-net sampling) that smooth dogfish were more abundant in Schooner Creek during 1987 prior to dredging of the adjacent shoal (Rountree, personal observ.).

It is noteworthy that smooth dogfish YOY were abundant in subtidal creek weir collections only during June–July (despite regular sampling from April to November) but were abundant in gill-net collections just outside the creeks through October (Figs. 3 and 4). Additionally, YOY captured by weirs in creeks tended to be smaller than those captured by other gears in bay habitats (Fig. 2). These patterns suggest that creek habitats are more important for newborn and smaller individuals than for older and larger individuals.

Foraging habits

The diet of YOY smooth dogfish comprised mainly benthic crustaceans and polychaetes (Table 3). Prey of YOY are typical of the dominant shallow estuarine faunal components in the area (Sogard and Able, 1991; Rountree and Able, 1992; Szedlmayer and Able, in press). The prevalence of *Crangon septemspinosa* and *Palaemonetes vulgaris* in the diet may explain the importance of the creek habitats to the smallest individuals during June and July because abundances of these two prey species exhibit a strong peak in marsh creeks at that time (Rountree and Able, 1992). Although smooth dogfish collected in shallow bay shoal and marsh creek habitats exhibited very full stomachs (Table 3; Fig. 8), the role of foraging behavior in the apparent tidal movements of smooth dogfish into these habitats is uncertain because of our lack of day samples. If the shoal and creek habitats were important foraging habitats, we would expect to see much higher gut fullness during ebb tide (when fishes are presumably leaving the shallows). Instead we observed slightly higher fullness values during flood tide.

The only published data on smooth dogfish feeding habits were produced more than seventy years ago (Fields, 1907; Breder, 1921). Breder (1921) also examined food habits of YOY from New Jersey (based on size information he gives) and reported a similar diet to that presented here. Bigelow and Schroeder (1953) later published a summary of dogfish food habits based on these studies but primarily considered the diet of adults. Interestingly, American lobster, *Homarus americanus,* figured prominently in the food habits of smooth dogfish taken from Cape Cod (Fields, 1907) but were not observed during our study presumably owing to the scarcity of settled juvenile lobsters in southern New Jersey estuaries (although pelagic-stage juveniles are common, [Able, unpubl. data]).

Conclusions

Young-of-the-year smooth dogfish use New Jersey estuaries as nurseries during late spring through fall, when pups grow rapidly to a size of 55–70 cm TL, prior to migration from the estuaries by the end of October. Smooth dogfish make tidal migrations into shallow bay shoal and tidal marsh creek habitats primarily at night, possibly to take advantage of high concentrations of small crustacean prey. As a result, shallow bay shoal and tidal marsh creek habitats appear to be critical nursery areas for smooth dogfish in New Jersey estuaries.

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Morphometry of juvenile and subadult *Loligo pealei* and *L. plei* from the northern Gulf of Mexico

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Abstract.—Two species of *Loligo* are abundant in northern Gulf waters: the long-finned squid, *Loligo pealei*, and the arrow squid, *Loligo plei*. Variability within species and similarities between the species often hamper accurate identification. The two species more closely resemble each other in areas of sympatry, and there is overlap in almost all of the diagnostic characters. Small specimens of *Loligo* are not easily identified, and there are few studies detailing their morphometry. Because of the taxonomic uncertainties associated with the identification of juveniles and subadults of *L. pealei* and *L. plei*, the species were differentiated by isoelectric focusing, and morphometric characters and indices of potential use in species separation were evaluated. Emphasis was placed on those taxonomic characters suitable for use in the field. Best discrimination between the two species was achieved with combinations of measurements of characters and calculated indices associated with cartilaginous structures (funnel cartilage length, gladius width [GW], nuchal cartilage length, and rachis width [RW]) and the shape of the gladius. An arbitrary cutoff in GW/RW ratio of 2.7 (ratio of the greatest width of the gladius to the width of the free rachis at the junction of the vane) correctly classified 100% of the *L. plei* and 91% of the *L. pealei*. The overall shape of the gladius (broader and more rounded in *L. pealei*), presence or absence of marginal ribs in the vane of the gladius, and the nature of the junction of the vane and free rachis (junction gradual and not distinct in *L. pealei*) were also useful in distinguishing the two species.

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Although squid are conspicuous components of the marine ecosystem and form a substantial portion of the invertebrate biomass in the northern Gulf of Mexico, many aspects of their life history and structural characteristics are poorly known. Three species of loliginid squid are abundant in northern Gulf waters (Rathjen et al., 1979): the brief squid, *Lolliguncula brevis* (Blainville 1823), the long-finned squid, *Loligo pealei* Lesueur 1821 (also known as the longfin inshore squid [Roper et al., 1984]), and the arrow squid, *Loligo plei* Blainville 1823. The lack of knowledge about the species of *Loligo* in the Gulf can, in part, be attributed to the difficulties in identifying juveniles. Recent interest in locating new or underutilized squid species, or both, and the recognition of the importance of documenting changes in marine biodiversity have increased emphasis on the need to improve taxonomic resolution in this important invertebrate group.

Although the adults of *L. pealei* and *L. plei* have been described by numerous authors (e.g. Haefner, 1964; LaRoe, 1967; Cohen, 1976; Roper et al., 1984), variability within species and similarities between the species often hamper precise identification. Species variability has been documented in the long-finned squid, *L. pealei*. Cohen (1976) noted that populations of long-finned squid varied widely both within and between geographic areas. In areas of sympatry with *L. plei*, the two species more closely resemble each other, and with the exception of gladius shape and the hectocotylus in adult males, there

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is overlap in all other diagnostic characters (Cohen, 1976). This problem is particularly acute in the northern Gulf of Mexico, where the two species are common. Hixon (1980) noted that all external characters and morphometric indices overlapped in immature specimens taken in waters off Texas. Difficulties in separating the species were best summarized by LaRoe (1967) who stated, "there are differences between the species, but there is a continuum between them in their range of variation for most characters; there appear to be no distinct boundaries to separate the two species."

The purpose of this study is to examine variability in morphological characteristics between juveniles and subadults of *L. pealei* and *L. plei* in the northern Gulf of Mexico and to determine diagnostic criteria for their identification. Emphasis is placed on taxonomic characters suitable for use in the field. Because of the taxonomic uncertainties associated with identification of immature and small specimens of the two *Loligo* species, an electrophoretic technique (isoelectric focusing) was used to establish species-specific protein patterns. Biochemical differentiation of species provided more accurate assessment of morphological variability between the two species. This contrasts with previous studies in which morphological variability was assessed by using specimens identified by morphological criteria.

Materials and methods

Field procedures

Squid samples were collected by personnel of the National Marine Fisheries Service, Mississippi Laboratories, Pascagoula, Mississippi, aboard the National Oceanic and Atmospheric Administration Ship RV *Oregon II*. Samples used here were obtained during the Southeast Area Monitoring and Assessment Program (SEAMAP) resource survey Cruise 93-03 (205), conducted from 6 June to 21 July 1993. Ottertrawl samples (n=230) were taken in an area from 88° to 97°30'W (Mobile, Alabama to Brownsville, Texas) in depths from 9 to 110 meters (Fig. 1). Station selection and field processing procedures followed established SEAMAP protocol.[1] All specimens of *Loligo*

[1] Nichols, S., and G. Pellegrin. 1989. Trends in catch per unit effort for 157 taxa caught in the Gulf of Mexico Fall Groundfish Survey, 1972–88. Summary Rep., Mississippi Laboratories, NMFS, NOAA, 158 p.

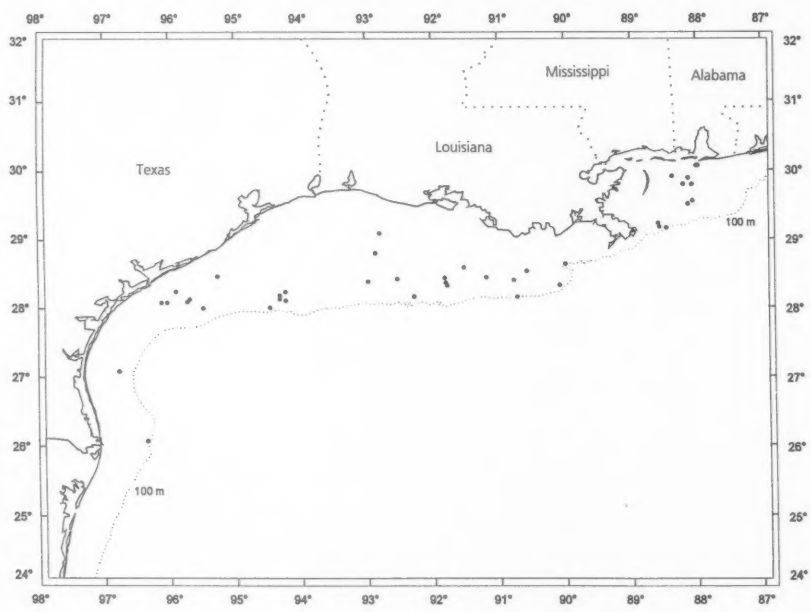

Figure 1

Location of trawl stations in the northern Gulf of Mexico where *Loligo pealei* and *Loligo plei* were collected.

were sorted from the trawl samples, counted, and weighed. They were frozen (–20°C) on board within two hours of capture to deter tissue degradation. Large, more readily identifiable squids were frozen separately for later use in biochemical determinations of species-specific protein patterns, whereas the smaller squids from each station were frozen together. All samples were sealed in polyethylene bags in which the air had been squeezed out to prevent freezer-burn during storage. The frozen squids were placed in chilled containers for transportation from the ship to the Gulf Coast Research Laboratory (GCRL), Ocean Springs, Mississippi, following completion of the cruise. Squids were stored at –20°C in the laboratory.

Laboratory procedures

Initial research efforts centered on establishing nonvariant protein patterns that could be used to separate the two *Loligo* species. Ten large specimens of each *Loligo* species (greater than 200-mm mantle length) were selected from the frozen samples and tentatively identified at GCRL with the morphological criteria provided by Bane and Wagner,[2] Voss (1956), LaRoe (1967), Cohen (1976), and Roper et al. (1984). These criteria included shape of the hectocotylus in males, overall body shape, the size and shape of the fins, and the dentition of the tentacular suckers. A sample of mantle tissue was removed from each squid, refrozen, and stored at –70°C. Frozen squids were shipped on dry ice to the National Museum of Natural History, Washington, D.C., for confirmation of field identifications. Following verification of identification of specimens based on morphological criteria, mantle tissue from each individual was analyzed electrophoretically and diagnostic protein bands were determined.

To evaluate morphometric parameters of potential value in field separation of *L. plei* and *L. pealei*, specimens of juvenile and subadult *Loligo* spp. (n=304) ranging in size from 29.0 to 238.0 mm mantle length (ML) were selected from the squid samples frozen in the field. Squids were selected from each of three geographic areas over the complete range of depths sampled (less than 18 m, 18–36 m, 37–55 m, 56–73 m, 74–110 m) within each area. Designation of geographic areas followed Nichols and Pellegrin[1]: Texas (Brownsville to Galveston), West Delta (Galveston, TX, to the Mississippi River), and East Delta (Mississippi River to Mobile, AL). Juvenile and subadult squids were selected from 41 stations without regard to probable species or sex. Specimens were thawed, individually numbered, and weighed to the nearest 0.1 g. Visual inspection for the presence of nidamental glands or the spermatophoric sac was used to separate females from males.

The diagnostic measurements and indices used by Voss (1956), Haefner (1964), Cohen (1976), and Hixon (1980) were reviewed for their potential usefulness in taxonomic resolution of the *Loligo* species. Eleven morphometric measurements and selected indices (ratios of measured characters) of potential value in separating species and sex within a species were determined (Table 1; Fig. 2).

Morphometric characters were measured with digital calipers to the nearest 0.1 mm. Because some individuals were damaged, the number of measured characters per individual varied. Squids >100.0 mm ML were not well represented in the sample aliquot. Large males of both *L. pealei* and *L. plei* were included in the aliquot, but there were few females of similar size. For that reason, size limitations were placed on the data used in regression analyses, with

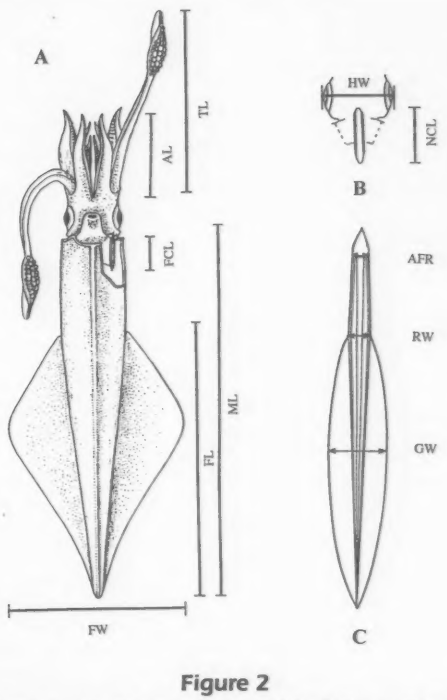

Figure 2

Morphometric characters measured for *Loligo pealei* and *Loligo plei* : (**A**) ventral view, modified from Roper et al. (1984); (**B**) head, dorsal view, from Cohen (1976); (**C**) gladius. Abbreviations are defined in Table 1.

[2] Bane, G. W., and A. Wagner. 1985. Key to important squids of the northern Gulf of Mexico. Coastal Fisheries Institute, Center for Wetland Resources, Louisiana State Univ., Baton Rouge, LA, LSU-CFI-85-21, 10 p.

the limits dependent upon the size-frequency distribution of the specimens. Size-class ranges for tests of sexual dimorphism were from 50.0 to 150.0 mm ML for *L. pealei* and from 40.0 to 110.0 mm ML for *L. plei*. When characters and indices were compared between the two species, squids from 20.0 to 150.0 mm ML were used in the analyses. Both individual characters and indices were regressed against mantle length to determine their potential value in differentiating species, or sex within a species, for squids of a given size.

After external measurements were recorded for each squid, the mantle was opened and the gladius removed. Drawings of the gladii were made by means of photocopies of the actual gladii as patterns. A piece of mantle tissue was taken from each squid, frozen immediately, and stored at –70°C. Specimens were refrozen and stored at –20°C.

Isoelectric focusing (IEF), a technique which separates proteins according to their isoelectric points along a continuous pH gradient (Righetti et al., 1990), was used to characterize mantle protein patterns. Mantle tissue was minced and then homogenized in BSS buffer (0.05 M Tris at pH 7.5, 0.25 M sucrose, 0.01 M KCl, 0.01 M $MgCl_2$, 0.001 M $CaCl_2$, 0.001 M phenylmethylsulfonyl fluoride) with an Ultra-Turex™ (Type TP 18/10 S1) homogenizer. The homogenate from each squid was centrifuged separately at 14,000 RPM (23,460 RCF) for 20 minutes at 4°C with a Beckman™ Model J-21C refrigerated centrifuge. The supernatants were recovered and frozen separately at –70°C. Total protein in each supernate was measured (Bio-Rad™ Bradford Protein Assay Kit) in order that the same amount of protein (35 µg) was loaded in each lane of the gel.

Isoelectric focusing separations were made in 0.5-mm polyacrylamide gels with an LKB Ultraphor™ apparatus. Proteins were separated with ampholytes of the 4.0–6.5 pH range by using 0.1 M glutamic acid as the analyte and 0.1 M beta-alanine as the catholyte. The gels were prefocused at 2,000 V for 30

Table 1

Morphometric characters and indices in *Loligo pealei* and *Loligo plei*.

Parameter	Definition[1]
Measured characters	
AFR (anterior free rachis)	Width of free rachis at terminus of marginal ribs
AL (arm length)	Length of right arm IV from proximalmost sucker to arm tip (left if right arm missing)
FCL (funnel cartilage length)	Greatest length of entire right funnel cartilage
FL (fin length)	Fin length from point on dorsal mantle midway between anterior fin insertion, to posterior body tip
FW (fin width)	Greatest width of both fins between lateralmost points
GW (gladius width)	Greatest width of gladius vane
HW (head width)	Greatest head width at level of eyes (head strongly ventrodorsally compressed between two fingers)
ML (mantle length)	Mantle length, from dorsal anterior margin to posterior end
NCL (nuchal cartilage length)	Greatest length of entire nuchal cartilage
RW (rachis width)	Width of gladius rachis at junction of vane
TL (tentacle length)	Length of right (left if right tentacle missing) tentacle from junction of arms III and IV to tip
W (weight)	Specimen wet weight to the nearest 0.1 g
Morphometric indices	
AL/ML	Arm length: mantle length index
FCL/ML	Funnel cartilage length: mantle length index
FL/ML	Fin length: mantle length index
FW/FL	Fin width: fin length index
FW/ML	Fin width: mantle length index
GW/ML	Gladius width: mantle length index
GW/RW	Gladius width: rachis width index
HW/ML	Head width: mantle length index
NCL/FCL	Nuchal cartilage length: funnel cartilage length index
NCL/ML	Nuchal cartilage length: mantle length index
RW/ML	Rachis width: mantle length index
TL/AL	Tentacle length: arm length index
TL/ML	Tentacle length: mantle length index
W/ML	Wet weight: mantle length index

[1] Modified from Cohen (1976).

minutes. The samples were then loaded and focused for 3 hours at 2,000 V. The gels were fixed, washed with destaining solution, and stained with Coomassie Blue R-250. They were washed again in destaining solution, dried, and photographed. Protein bands from the juvenile and subadult squids were compared with protein bands from the positively identified adult specimens for species identification.

Statistical analysis of data

Two approaches were used in morphometric analysis of data: comparisons were made between species and by sex within each species. All data were analyzed with Statgraphics Plus, Version 7.1 computer software. Student's *t*-test (α=0.05) was used to compare the means of indices to determine if any index could be used to distinguish between the two species or between sexes within a species. Both linear and multiplicative regression techniques were employed to examine the relation of each measured character and each index (dependent variable) to mantle length (independent variable). Correlation coefficients (r) and coefficients of determination (r^2) were calculated for each regression to measure strength of the relationship and goodness of fit of the calculated regression line, respectively.

Coefficients of determination were considered high when 85% of the total observed variability was accounted for by the mathematical model. Tests were conducted for differences in the slopes of the regression lines. The null hypothesis was that there was no significant difference (α>0.05) between the slopes. A discriminant analysis was employed to identify the relative contribution of measured characters or indices, or both, in discriminating between the two species. For each individual, the characters and indices were entered with their respective species classification codes. Analyses were performed as follows: 1) all characters, 2) all indices, and 3) selected characters or indices, or both (singly or in combination), based on discriminant function coefficients. From these analyses, characters or indices (or both), were ranked by comparing their percentage success in species differentiation.

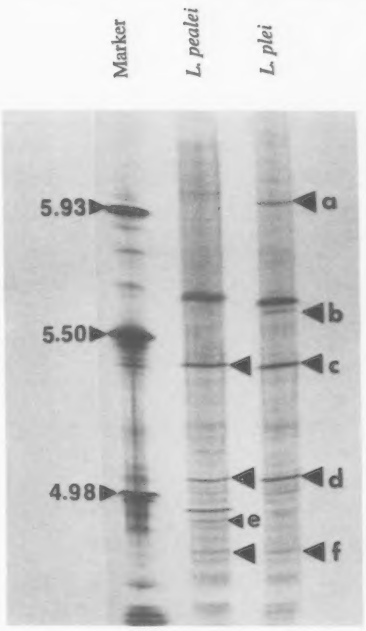

Figure 3
Protein electrophoretic patterns of mantle tissue from *Loligo pealei* and *Loligo plei* (numbers=pH, letters=protein bands).

Table 2
Isoelectric points (pH) used to separate *Loligo pealei* and *Loligo plei*.

Band	pH	Species
a[1]	5.97	*L. plei*
b[1]	5.60	*L. plei*
c	5.41	*L. plei, L. pealei*
d	5.02	*L. plei, L. pealei*
e[2]	4.89	*L. pealei*
f	4.76	*L. plei, L. pealei*

[1] Unique to *L. plei*.
[2] Unique to *L. pealei*.

Results

Biochemical analyses

Isoelectric focusing patterns of mantle tissue proteins are shown in Figure 3. Proteins used to differentiate between the species were labeled *a* through *f* according to their decreasing order of isoelectric points (Table 2). Both species had unique protein bands and were easily separated: bands *a* and *b* were unique to *L. plei* and band *e* to *L. pealei*. Bands *c*, *d*, and *f* were shared by both species.

General description of juveniles and subadults

In fresh specimens, the chromatophores of the mantle generally are red in color in *L. plei* and brown in *L.*

pealei. Color, however, is not a reliable means of separating the species. Well-defined lines of chromatophores ("flame stripes") occur on the ventral surface of the mantle in large males of *L. plei*; however, specimens of *L. pealei* also may have a similar, though less defined, color pattern. The mantle is long, slender, and cylindrical in both *L. pealei* and *L. plei*, but the posterior end of the mantle is more acutely pointed in *L. plei*. Juvenile and subadult *L. pealei* are more robust than *L. plei* of similar mantle length: the head and eyes of the former species are moderately large and the arms and tentacles are thick, muscular, and long. The more robust character of *L. pealei* is particularly evident when compared with *L. plei* of the same mantle length. The fins are rhomboidal in shape in both species.

Fin length as a percentage of mantle length is variable in individuals of both species, but it is generally greater in *L. pealei* than in *L. plei* in specimens of similar mantle length (Table 3). Mean fin length in relation to mantle length of *L. pealei* was 50% in the size class 90.0 to 99.9 mm, and the mean ratio increased as mantle length increased. However, fin length to mantle length ratio of individual *L. pealei* could be 50% in specimens as small as 70.0 mm ML; the ratio of FL to ML was not consistently 50% or greater until the individual mantle length reached 110.0 mm. For *L. plei*, the ratio of fin length to mantle length was less than 50% for individual squid smaller than the 120.0 to 129.9 mm ML size class. Mean fin length to mantle length did not exceed 50% until size class 140.0 to 149.9 mm ML.

Morphometric analyses

Individual measurements were taken of 304 juvenile and subadult squids (*L. pealei*, n=151; *L. plei*, n=153). All specimens were immature according to the maturity classification scheme of Macy (1982). The relationships between fin length and mantle length, fin width and mantle length, and rachis width and mantle length were best represented by the linear model. The relationships between weight, head width, funnel cartilage length, nuchal cartilage length, gladius width, arm length, and tentacle length, with mantle length as the independent variable, were best represented by the multiplicative model. All indices were best represented by the linear model.

Sexual dimorphism

Loligo pealei Sex could be determined for only 36% of the specimens identified as *L. pealei* (n=62). Males

Table 3

Fin length in relation to mantle length in *Loligo pealei* and *Loligo plei*.

Mantle length (mm)	Fin length as % of mantle length							
	L. pealei				*L. plei*			
	n	Mean	±SD	Range	*n*	Mean	±SD	Range
20–29.9	0				1	20.7		
30–39.9	1	37.6			9	27.2	±3.3	18.1–29.5
40–49.9	27	37.6	±2.6	31.7–42.6	22	31.5	±3.1	26.3–37.6
50–59.9	47	40.6	±2.8	33.3–45.3	44	34.6	±2.3	26.9–38.7
60–69.9	16	43.2	±1.9	40.5–46.4	41	36.7	±2.1	33.1–40.3
70–79.9	9	46.2	±2.4	43.5–50.8	12	39.2	±2.0	35.8–42.9
80–89.9	7	47.0	±2.9	41.7–52.2	9	41.7	±1.3	39.9–43.9
90–99.9	13	50.0	±3.9	42.5–57.1	5	44.3	±2.9	40.0–47.5
100–109.9	5	50.4	±1.8	47.8–53.2	3	46.0	±2.1	43.5–48.7
110–119.9	4	52.0	±1.9	50.4–55.2	0			
120–129.9	8	53.4	±3.1	49.7–58.6	3	47.8	±1.3	46.6–49.6
130–139.9	4	55.8	±1.6	53.4–57.6	1	47.5		
140–149.9	3	54.9	±0.9	54.1–56.1	1	50.5		
150–159.9	1	54.3			1	51.7		
160–169.9	0				1	53.4		
170–179.9	2	56.2	±1.7	54.5–57.9	0			
180–189.9	0				0			
190–199.9	2	59.5	±0.5	59.0–60.0	0			
≥200	2	59.8	±1.5	58.3–61.3	0			

used in statistical analyses ranged in size from 50.0 to 147.0 mm and females from 64.0 to 140.0 mm ML. Results of statistical analyses of tests of sexual dimorphism for characters and indices are shown in Table 4.

Coefficients of determination (r^2) were high for both males and females for AL, FCL, FL, GW, NCL, RW, and W when regressed on mantle length. The slopes of the regression lines were similar between sexes for W and GW, but females were heavier than males (Fig. 4) and had a broader gladius (Fig. 5). There were also no significant differences between males and females in the slopes of the regression lines for AL, FCL, FL, NCL, and RW, and the 95% confidence intervals of the regression intercepts overlapped. Fin width was highly correlated with ML only in females. Overlap occurred in all measured characters.

Significant differences were found in the slopes of the regression lines only for W/ML. With the exception of W/ML in females, all indices had low coefficients of determination. Means of the indices of FW/ML, GW/ML, GW/RW, and RW/ML were significantly higher in females than in males; however, overlap was high.

Loligo plei Sex could be determined for 51% of the specimens identified as *L. plei* (n=73). Males used in statistical analyses ranged in size from 52.0 to 107.0 and females from 46.0 to 101.0 mm ML. Results of statistical analyses of tests of sexual dimorphism for characters and indices are shown in Table 5.

No significant differences were found between the sexes in the slopes of the regression lines for any of the characters. Weight (Fig. 6) and GW (Fig. 7) were highly correlated to ML in both males and females; however, there was no significant difference in the slopes of the regression lines, and the 95% confidence intervals of the regression intercepts overlapped. Females were heavier than males of similar length, and the gladius was broader in female specimens. Fin length and RW were also highly correlated with ML but, as with W and GW, there was no significant difference in the slopes of the regression lines and the 95% confidence intervals of the regression intercepts overlapped. Fin width, FCL, and NCL were highly correlated with mantle length only in males.

With the exception of FCL/ML in males, all indices had low coefficients of determination. There were significant differences in the means of FW/FL,

Table 4

Statistical tests of sexual dimorphism in *Loligo pealei* (sample sizes are given in parentheses). Abbreviations are defined in Table 1. NS = not significant.

	AL	FCL	FL	FW	GW		
Male (r^2)	0.85 (27)	0.92 (28)	0.97 (28)	0.81 (28)	0.95 (28)		
Female (r^2)	0.88 (18)	0.93 (19)	0.96 (19)	0.90 (19)	0.93 (19)		
Slope test	NS	NS	NS	NS	NS		
	HW	NCL	RW	TL	W		
Male (r^2)	0.62 (28)	0.95 (28)	0.90 (28)	0.50 (22)	0.96 (28)		
Female (r^2)	0.67 (19)	0.96 (19)	0.92 (19)	0.62 (15)	0.98 (19)		
Slope test	NS	NS	NS	NS	NS		
	AL/ML	FCL/ML	FL/ML	FW/FL	FW/ML	GW/ML	GW/RW
Male (r^2)	0.00 (27)	0.64 (28)	0.64 (28)	0.56 (28)	0.00 (28)	0.17 (28)	0.03 (28)
Female (r^2)	0.15 (18)	0.74 (19)	0.53 (19)	0.20 (19)	0.05 (19)	0.00 (19)	0.05 (19)
Slope test	NS	NS	NS	NS	NS	NS	NS
t-test of means	NS	NS	NS	NS	P=0.0097	P<0.0001	P=0.0076
Means (M, F)	0.58, 0.60	0.15, 0.16	0.50, 0.51	1.08, 1.14	0.53, 0.58	0.15, 0.17	2.99,3.17
	HW/ML	NCL/FCL	NCL/ML	RW/ML	TL/AL	TL/ML	W/ML
Male (r^2)	0.50 (28)	0.49 (28)	0.14 (28)	0.33 (28)	0.21 (22)	0.21 (22)	0.87 (28)
Female (r^2)	0.41 (19)	0.29 (19)	0.56 (19)	0.08 (19)	0.09 (15)	0.25 (15)	0.95 (19)
Slope test	NS	NS	NS	NS	NS	NS	P=0.0145
t-test of means	NS	NS	NS	P=0.0241	NS	NS	NS
Means (M, F)	0.21, 0.22	1.22, 1.20	0.18, 0.19	0.050, 0.052[1]	2.67, 2.68	1.55, 1.61	0.38, 0.41

[1] Difference between means is small but t-test is significant.

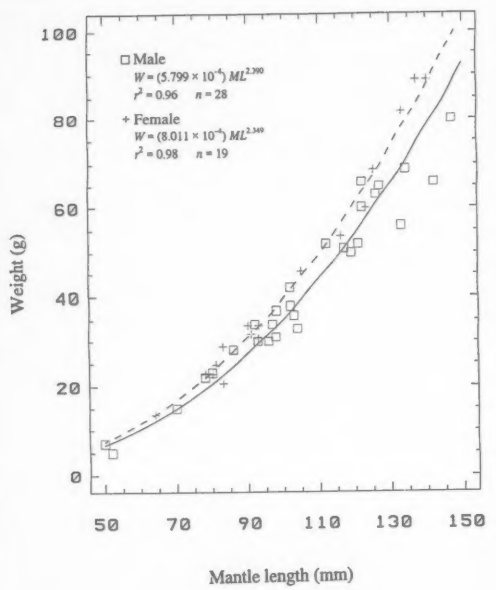

Figure 4

Regression of weight (W) on mantle length (ML) for male and female *Loligo pealei*.

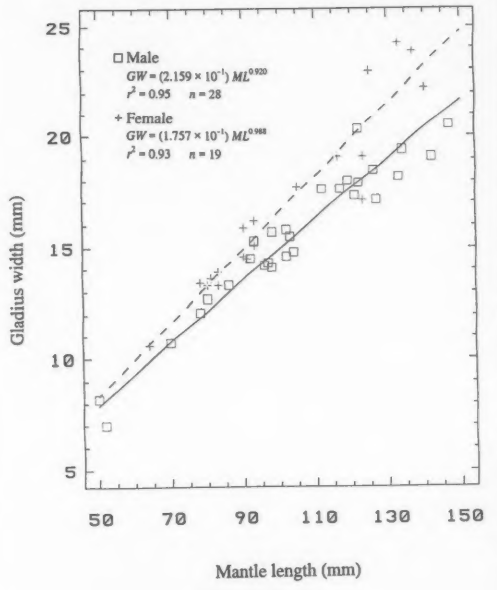

Figure 5

Regression of gladius width (GW) on mantle length (ML) for male and female *Loligo pealei*.

Table 5

Statistical tests of sexual dimorphism in *Loligo plei* (sample sizes are given in parentheses). Abbreviations are defined in Table 1. NS = not significant.

	AL	FCL	FL	FW	GW		
Male (r^2)	0.73 (14)	0.88 (14)	0.97 (14)	0.90 (14)	0.96 (14)		
Female (r^2)	0.60 (51)	0.53 (51)	0.97 (51)	0.83 (50)	0.86 (50)		
Slope test	NS	NS	NS	NS	NS		
	HW	NCL	RW	TL	W		
Male (r^2)	0.59 (14)	0.91 (14)	0.90 (14)	0.39 (9)	0.93 (14)		
Female (r^2)	0.28 (51)	0.66 (51)	0.86 (50)	0.58 (36)	0.92 (51)		
Slope test	NS	NS	NS	NS	NS		
	AL/ML	FCL/ML	FL/ML	FW/FL	FW/ML	GW/ML	GW/RW
Male (r^2)	0.59 (14)	0.91 (14)	0.80 (14)	0.49 (14)	0.01 (14)	0.39 (14)	0.06 (14)
Female (r^2)	0.03 (51)	0.61 (51)	0.74 (51)	0.50 (50)	0.01 (50)	0.10 (50)	0.09 (50)
Slope test	NS	NS	NS	NS	NS	NS	NS
t-test of means	NS	NS	NS	P=0.0322	NS	P<0.0001	P=0.0012
Means (M, F)	0.50, 0.49	0.14, 0.14	0.39, 0.38	1.13, 1.22	0.44, 0.46	0.13, 0.14	2.08, 2.24
	HW/ML	NCL/FCL	NCL/ML	RW/ML	TL/AL	TL/ML	W/ML
Male (r^2)	0.69 (14)	0.51 (14)	0.61 (14)	0.41 (14)	0.19 (9)	0.54 (9)	0.73 (14)
Female (r^2)	0.45 (51)	0.21 (51)	0.50 (51)	0.36 (50)	0.00 (36)	0.10 (36)	0.77 (51)
Slope test	NS	NS	NS	NS	NS	NS	NS
t-test of means	NS	NS	NS	NS	NS	NS	NS
Means (M, F)	0.20, 0.20	1.17, 1.17	0.16, 0.17	0.06, 0.06	3.08, 3.18	1.52, 1.58	0.16, 0.15

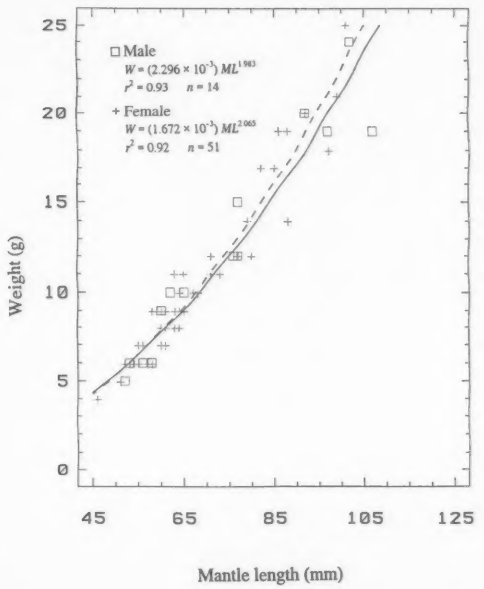

Figure 6

Regression of weight (W) on mantle length (ML) for male and female *Loligo plei*.

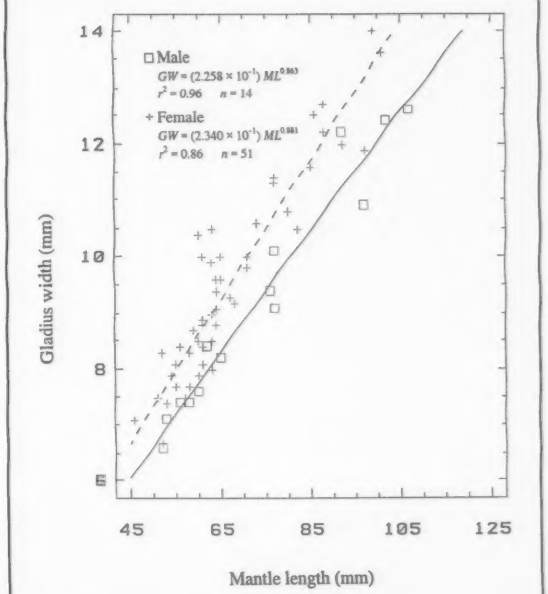

Figure 7

Regression of gladius width (GW) on mantle length (ML) for male and female *Loligo plei*.

GW/ML, and GW/RW, and means were higher for these indices in females. Overlap occurred in all indices.

Species comparisons

The specimens of *Loligo pealei* used in species comparisons ranged in size from 37.0 to 147.0 mm ML, whereas specimens of *L. plei* ranged in size from 29.0 to 148.0 mm ML. Results of statistical analyses of tests of species comparisons for characters and indices are shown in Table 6.

There were significant differences in the slopes of the regression lines for all characters except HW and RW. Variability in W was low in both species and overlap occurred in only the smaller size classes (Fig. 8). Coefficients of determination also were high for FL, FW, GW, NCL, and RW in both species; however, overlap occurred in all characters (Figs. 9–13, respectively). Arm length and FCL were highly correlated with mantle length only in *L. pealei*.

Significant differences occurred in the slopes of the regression lines for the following indices: AL/ML, FCL/ML, FL/ML, FW/FL, GW/ML, NCL/ML, RW/ML, TL/AL, and W/ML. With the exception of W/ML for *L. pealei*, the coefficients of determination were low. Although little of the variability was explained by the regression lines for GW/RW regressed on mantle length, a scatter plot of the GW/RW ratios showed minimal overlap; thus this index may have predictive value in separating juveniles and subadults of the two species (Fig. 14). Significant differences were found between mean indices for all but FW/FL and NCL/FCL. Mean indices were greater in *L. pealei* for all ratios with the exception of RW/ML and TL/AL.

Overlap was high for all indices with the exception of GW/RW. Both the scatter plot (Fig. 14) and frequency histogram (Fig. 15) showed relatively low overlap in the GW/RW indices. The GW/RW index was higher for *L. pealei* in most instances. Only 9% of the *L. pealei* specimens were in the range of overlap, and this overlap was more common in smaller squid, including a distinct mode of small *L. pealei* within the GW/RW range of *L. plei* (Fig. 15).

Discriminant function coefficients were highest for cartilaginous structures. Results of discriminant analyses showed that no character, index, or combination of the two, classified *L. pealei* with 100% accuracy (Fig. 16; Table 7). Rachis width in combination with NCL enabled separation at an accuracy level of 93%, and in combination with FCL or GW separated 95% of the specimens of *L. pealei*. Indices that allowed separation of *L. pealei* from *L. plei* at accuracy levels of 92% and above included the GW/RW

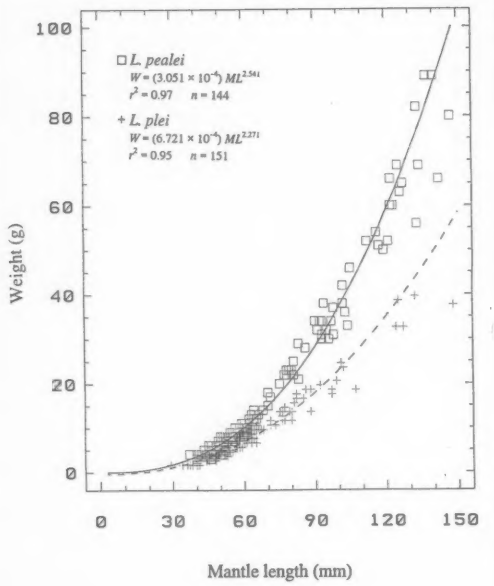

Figure 8

Regression of weight (W) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

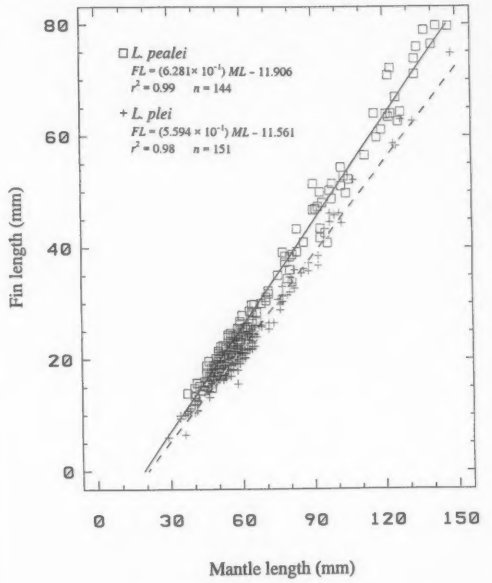

Figure 9

Regression of fin length (FL) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

Table 6

Species comparison of characters and indices for *Loligo pealei* and *Loligo plei* (sample sizes are given in parentheses). Abbreviations are defined in Table 1. NS = not significant.

	AL	FCL	FL	FW	GW		
L. pealei (r^2)	0.94 (141)	0.95 (144)	0.99 (144)	0.93 (143)	0.96 (143)		
L. plei (r^2)	0.75 (151)	0.84 (151)	0.98 (151)	0.91 (150)	0.90 (150)		
Slope test	P=0.0130	P<0.0001	P<0.0001	P<0.0001	P=0.0022		
	HW	NCL	RW	TL	W		
L. pealei (r^2)	0.71 (143)	0.97 (144)	0.94 (144)	0.84 (106)	0.97 (144)		
L. plei (r^2)	0.66 (151)	0.91 (151)	0.89 (150)	0.66 (109)	0.95 (151)		
Slope test	NS	P<0.0001	NS	P=0.0133	P<0.0001		
	AL/ML	FCL/ML	FL/ML	FW/FL	FW/ML	GW/ML	GW/RW
L. pealei (r^2)	0.00 (141)	0.65 (144)	0.78 (144)	0.44 (143)	0.01 (143)	0.02 (143)	0.02 (143)
L. plei (r^2)	0.10 (151)	0.61 (151)	0.76 (151)	0.48 (150)	0.00 (150)	0.17 (150)	0.00 (150)
Slope test	P=0.0011	P=0.0001	P=0.0102	P=0.0017	NS	P=0.0006	NS
t-test of means	P<0.0001	P<0.0001	P<0.0001	NS	P<0.0001	P<0.0001	P<0.0001
Means (*L. pealei*, *L. plei*)	0.59, 0.49	0.17,0.15	0.44, 0.36	1.27, 1.24	0.55, 0.44	0.16, 0.14	3.13, 2.18
	HW/ML	NCL/FCL	NCL/ML	RW/ML	TL/AL	TL/ML	W/ML
L. pealei (r^2)	0.19 (143)	0.44 (144)	0.33 (144)	0.00 (144)	0.34 (105)	0.36 (106)	0.95 (144)
L. plei (r^2)	0.47 (151)	0.26 (151)	0.45 (151)	0.17 (150)	0.00 (109)	0.06 (109)	0.86 (151)
Slope test	NS	NS	P<0.0001	P<0.0001	P=0.0005	NS	P<0.0001
t-test of means	P<0.0001	NS	P<0.0001	P<0.0001	P=0.0080	P<0.0001	P<0.0001
Means (*L. pealei*, *L. plei*)	0.25, 0.20	1.15, 1.17	0.19, 0.17	0.05, 0.06	2.98, 3.13	1.75, 1.51	0.23, 0.13

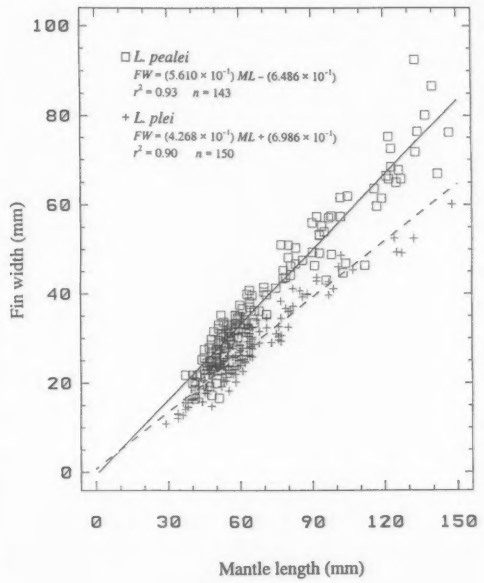

Figure 10

Regression of fin width (FW) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

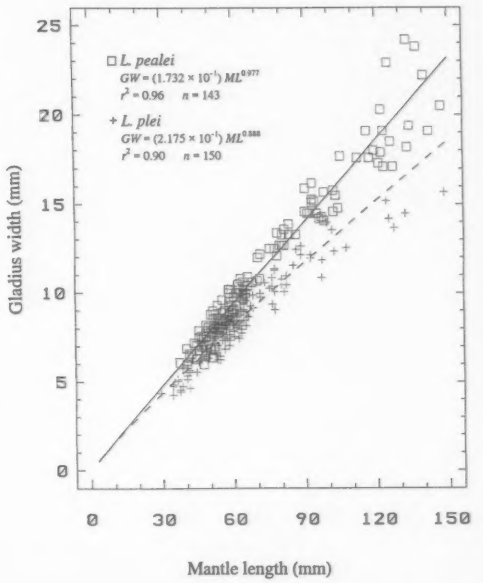

Figure 11

Regression of gladius width (GW) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

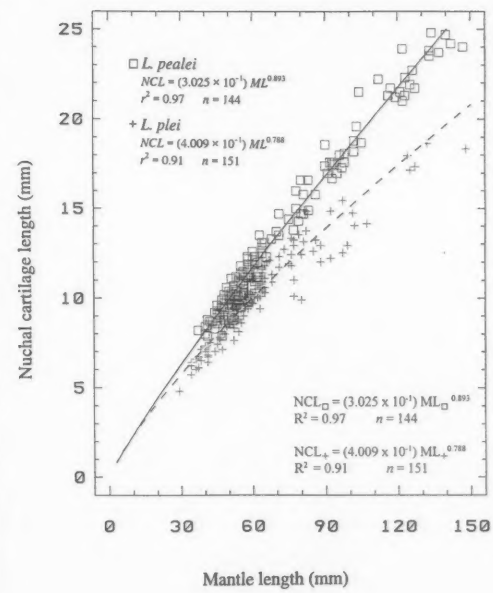
□ L. pealei
NCL = (3.025 × 10⁻¹) ML^0.893
r² = 0.97 n = 144
+ L. plei
NCL = (4.009 × 10⁻¹) ML^0.788
r² = 0.91 n = 151
NCL□ = (3.025 x 10⁻¹) ML□ 0.893
R² = 0.97 n = 144
NCL+ = (4.009 x 10⁻¹) ML+ 0.788
R² = 0.91 n = 151
Nuchal cartilage length (mm)
Mantle length (mm)

Figure 12

Regression of nuchal cartilage length (NCL) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

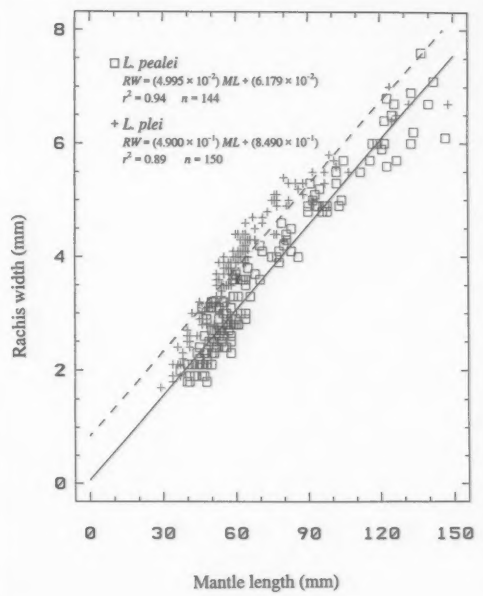

Figure 13

Regression of rachis width (RW) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

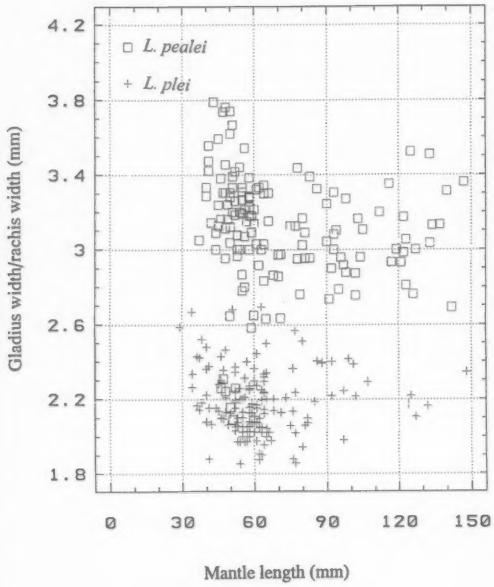

Figure 14

Cluster plot of gladius width/rachis width (GW/RW) on mantle length (ML) for *Loligo pealei* and *Loligo plei*.

ratio alone and this index in combination with either FCL/ML, GW/ML, NCL/ML or RW/ML. The RW/ML ratio in combination with FCL/ML, GW/ML, or NCL/ML provided for similar levels of accuracy. In contrast, *L. plei* could be correctly classified at 100% accuracy with the combination of FCL and RW (Table 8). Correct classification levels of 98% and 99% were obtained when RW was combined with GW or NCL, respectively. High levels of separation in *L. plei* also occurred with the indices GW/RW or RW/ML in combination with selected indices (Table 8). With the GW/RW index alone, 98% of the *L. plei* specimens were correctly classified.

Structure of the gladius

The gladius in *L. pealei* is broad and feather-shaped in all specimens (Fig. 17, A and B). The gladius is more rounded in females than in males. The greatest gladius width occurs at the mid-point of the vane. The ratio of the greatest width of the gladius to the greatest width of the rachis ranges from 2.26 to 3.36 in males and from 2.74 to 3.52 in females. The rachis has a single median rib with marginal ribs on each side that fuse in the posterior 1/3 of the rachis. The anterior and posterior tips of the rachis are pointed. The vane is broad and without ribs. The

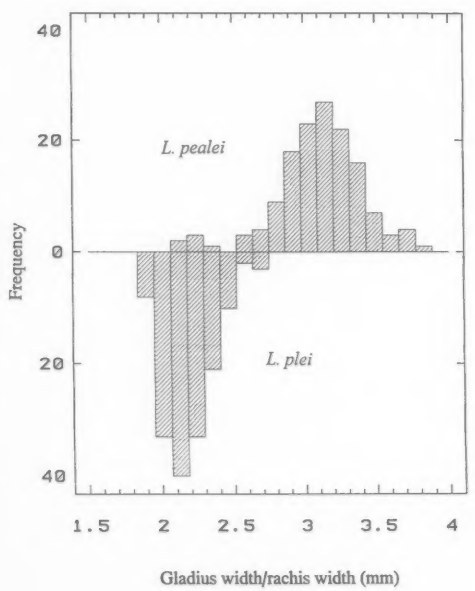

Figure 15

Frequency histogram for gladius width/rachis width (GW/RW) for *Loligo pealei* and *Loligo plei*.

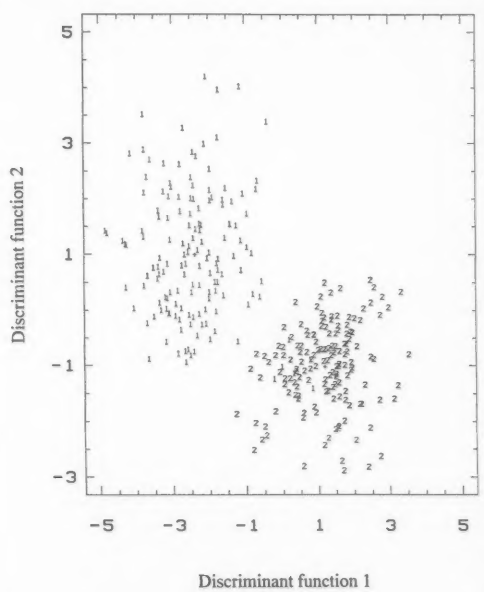

Figure 16

Discriminant analysis plot for *Loligo pealei* (function 1) and *Loligo plei* (function 2).

margins of the vane are curved, thin, and converge both anteriorly and posteriorly. The junction of the rachis and the vane is gradual and not distinct. The free rachis tapers anteriorly from the junction of the vane to the terminus of the marginal ribs. The ratio of AFR/RW ranges from 0.633 to 1.100 in males and from 0.684 to 0.946 in females.

The gladius in *L. plei* is slender and sword-shaped in all specimens (Fig. 17, C and D). The greatest gladius width in males occurs in the anterior 1/4 of the vane. In females, the greatest width occurs near the mid-point of the vane. The ratio of the greatest width of the gladius to the greatest width of the rachis ranges from 1.85 to 2.34 in males and from 1.98 to 2.69 in females. One median rib occurs on the rachis with marginal ribs on each side that fuse in the posterior 1/3 of the rachis. Anterior and posterior tips of the rachis are very pointed. The vane tapers both anteriorly and posteriorly. The junction of the rachis and the vane is abrupt and distinct. The vane in both sexes has marginal ribs that gradually curve inward, anterior to the midpoint of the vane. The lateral margins of the vane are usually straighter in males than in females. The posterior tip of the rachis is less flexible than the anterior tip owing to the convergence and fusion of the ribs of the vane and the rachis. The thickness of the ribs in both the rachis and the vane increases with increasing size of the specimen. The ribs usually are more pronounced in males than in females. The ribs in the vane of small specimens are distinguishable only as a color variation when held up to the light. The free rachis tapers from the junction of the vane to the terminus of the marginal ribs. The ratio of AFR/RW ranges from 0.701 to 1.043 in males and from 0.829 to 1.360 in females.

Table 7

Percent *Loligo pealei* separated from *Loligo plei* by using cartilaginous structures (sample sizes are given in parentheses). Abbreviations are defined in Table 1.

	FCL	GW	NCL	RW	
FCL	49 (151)	61 (150)	69 (151)	95 (151)	
GW		46 (150)	46 (150)	95 (150)	
NCL			45 (151)	93 (151)	
RW				61 (151)	
	FCL/ML	**GW/ML**	**GW/RW**	**NCL/ML**	**RW/ML**
FCL/ML	72 (151)	81 (150)	95 (150)	79 (151)	93 (151)
GW/ML		83 (150)	92 (150)	86 (150)	95 (150)
GW/RW			92 (150)	93 (150)	93 (150)
NCL/ML				77 (151)	92 (151)
RW/ML					88 (151)

Table 8

Percent *Loligo plei* separated from *Loligo pealei* by using cartilaginous structures (sample sizes are given in parentheses). Abbreviations are defined in Table 1.

	FCL	GW	NCL	RW	
FCL	83 (153)	80 (152)	80 (153)	100 (152)	
GW		79 (152)	82 (152)	98 (152)	
NCL			82 (153)	99 (152)	
RW				53 (152)	
	FCL/ML	**GW/ML**	**GW/RW**	**NCL/ML**	**RW/ML**
FCL/ML	73 (153)	82 (152)	98 (152)	75 (153)	95 (152)
GW/ML		77 (152)	98 (152)	81 (152)	98 (152)
GW/RW			98 (152)	99 (152)	99 (152)
NCL/ML				75 (153)	97 (152)
RW/ML					87 (152)

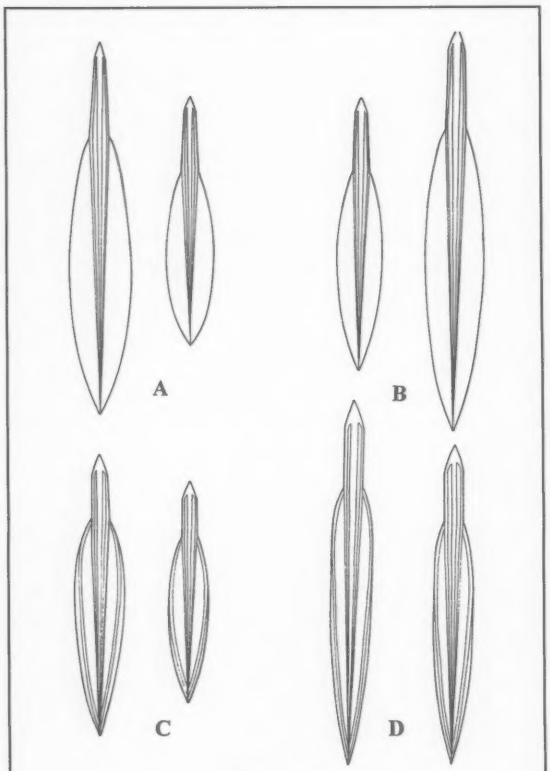

Figure 17
Illustrations of gladii traced from photocopies: *Loligo pealei* (**A**) female (**B**) male; *Loligo plei* (**C**) female (**D**) male.

Discussion

Isoelectric focusing of mantle proteins seems to provide a reliable means of distinguishing between the two species of *Loligo* in the Gulf of Mexico and to enable accurate identification of small, immature specimens. Garthwright et al. (1989) also biochemically separated *L. plei* and *L. pealei* but used the technique of horizontal starch gel electrophoresis. Morphometric analyses provided information on sexual dimorphism within the species and on species differences and similarities in specimens from the northern Gulf of Mexico, already identified to species by means of IEF.

Comparisons of morphometric characters and indices between males and females of each species were made in an effort to determine their value as a rapid means for fishery biologists to distinguish the sexes in the field. Although statistically significant differences were evident in many of the selected morphometric characters and indices, both between sexes within a species and between species, the differences were small and overlap usually was high. The majority of squids examined in this study were between 40.0 and 80.0 mm ML, and greatest overlap in characters and indices occurred in this size range.

Tests of sexual dimorphism in measured characters regressed against mantle length for *L. pealei* indicated no significant differences between males and females in the slopes of the lines for W and GW. Females were heavier than males and the GW was broader in females than in males in all size classes. Weight and GW also were highly correlated to ML in both males and females of *L. plei*; however, no significant difference existed in the slopes of the lines, and the 95% confidence intervals of the regression intercepts overlapped. Differences in weight between males and females were more pronounced in *L. pealei*. Haefner (1964) noted little difference in the weight–length relationship between males and females of *L. pealei* below 95 mm ML; however, at mantle lengths greater than 95 mm ML, females began to outweigh males. Hixon (1980) also found that the rate of increase in weight per unit increase in mantle length was faster in females than in males. Both Haefner (1964) and Hixon (1980) attributed this faster rate of increase in females to sexual maturation and the increase in weight of the female reproductive structures. For northernmost populations of *L. pealei* off New England, females less than 170.0 mm ML generally weighed less than males (Lange and Johnson, 1981). Maturation at smaller sizes in southern populations of long-finned squid could account for this difference in the weight–length relationship between females and males in comparisons of data for northern and southern populations. Both Cohen (1976) and Hixon (1980) noted that *L. pealei* seems to mature at smaller sizes in the warmer portion of its range. Width of the gladius also has been linked to sexual maturation in female *Loligo*. Cohen (1976) noted that in mature females the broadest portion of the gladius, the vane, covers the full ovary and may provide support and protection for the eggs. In the present study, the gladius was broader in females of both species.

Although there were differences in morphometric characters and indices between sexes within a species, these differences were subtle and usually were more apparent in larger specimens. The high overlap both in measured characters and in indices precluded their use as a reliable means of distinguishing the sexes in juvenile and subadult specimens. Gender-specific morphological characters (e.g. hectocotylus or sexual organs) appear to be the only precise means of differentiating males and females of the two species. In those specimens in which these characters are undeveloped, no way was discovered to distinguish between the sexes.

Juvenile and subadult *L. pealei* and *L. plei* overlapped in all measured characters. For those characters in which there was a significant difference in the slopes of the regression lines and for which the coefficients of determination were high (FL, FW, GW, NCL, and W), the overlap generally was higher in the smaller size classes. Differences in W, NCL, and GW were more pronounced in larger specimens. Increases in measured characters per unit increase of mantle length were higher in *L. pealei*.

Both Cohen (1976) and LaRoe (1967) reported differences in fin lengths between *L. pealei* and *L. plei* and suggested that this character could be used to differentiate between the two species. Cohen (1976) found that fin length in relation to mantle length was similar in both species in small specimens. However, she noted that fin length was equal to or greater than half the mantle length of *L. pealei* when mantle length exceeded 55.0 mm, whereas fin length was equal to or greater than half the mantle length in specimens of *L. plei* only after mantle length exceeded 95.0 mm. Fin length/mantle length proportions in the present study corroborate these data for juvenile and subadult specimens from the northern Gulf of Mexico. Fin lengths were less than 50% of the mantle length in both species in all specimens under 70.0 mm ML. In *L. pealei*, the mean fin length of specimens from 90.0 to 99.9 mm ML was equal to 50% of the mantle length, and this percentage increased with increasing size. Fin length in relation to mantle length was 50% in *L. plei* only at mantle lengths of 120.0 mm and larger. LaRoe (1967) also listed width of the gladius and length of the funnel cartilage as useful characters to separate the species; however, Cohen (1976) noted that the overlap in values for these characters negated their usefulness. The present data show overlap in GW in all but the larger size classes. Overlap in FCL was more prevalent in smaller size classes, but in specimens greater than 90.0 mm ML, it may be a useful character.

The shape of the gladius and the area of the junction of the vane and free rachis were distinct in both species over the size range of individuals examined. The gladius in *L. pealei* was broader and more rounded than was the gladius in *L. plei*. It was feather-shaped in all specimens and the vane was without ribs. The junction of the vane and the free rachis was gradual and not distinct. The gladius in *L. plei* was more slender, elongated, and resembled a sword or dagger in shape. Ribs in the vane were more obvious in larger specimens. The lateral margins of the vane were usually straighter and the ribs in the vane were more pronounced in males than in females. The junction of the vane and free rachis was abrupt and distinct.

The best discrimination between the two *Loligo* species was based on combinations of measurements of the characters and calculated indices associated with cartilaginous structures. Funnel or nuchal cartilage lengths combined with rachis width measurements or indices enabled greatest percent separation of the species. Characters and indices based on gladius shape also had high percentage levels of separation. Highest correct classification of *L. pealei* (95%) by discriminant analysis was achieved by combining RW with either FCL or GW or by combining the GW/ML and RW/ML indices. *Loligo plei* were classified with 100% accuracy by combining FCL and RW.

Numerous studies cite the GW/RW ratio as a reliable index for species differentiation. Roper et al. (1984) summarized taxonomic data for the two species and reported GW/RW ratios from 2.4 to 3.7 for *L. pealei* and from 1.5 to 2.4 for *L. plei*. Cohen (1976), Whitaker (1978), and Hixon (1980) also used the GW/RW index to distinguish the two species of *Loligo* and used the ratio of 2.4 to differentiate between the species: below 2.4 for *L. plei* and above 2.4 for *L. pealei*. The present study is the first to use IEF to identify juvenile and subadult *L. pealei* and *L. plei* and thus provides a more accurate base from which to assess morphological variation between the species. The GW/RW ratios in the present study ranged from 1.9 to 2.7 for *L. plei* and from 2.1 to 3.8 for *L. pealei*. Separation of the species was best accomplished with a GW/RW ratio of 2.7. Applying the ratio of 2.4 to the present data resulted in overlap in both species; 10% of the *L. plei* had an index greater than 2.4, and 4% of the *L. pealei* had an index below 2.4. By using 2.7 as the critical value, all the *L. plei* were separated and 91% of the *L. pealei* could be identified. Hixon (1980) also found specimens of *L. plei* with GW/RW ratios above 2.4. He identified 21 mature females and one male *L. plei* from Texas waters with GW/RW indices ranging from 2.4 to 2.9. He attributed the greater index in the females to the wider vane associated with sexually mature individuals. This does not explain the higher GW/RW indices recorded for some specimens of *L. plei* in this study, because all individuals were immature. Also puzzling are the specimens of *L. pealei* with GW/RW ratios below 2.7. Because all specimens in the present study were identified biochemically, errors in identification should be negligible. According to Cohen (1976), *L. pealei* is composed of morphologically variable populations and greater variation occurs in areas where *L. pealei* co-occurs with *L. plei*. In these areas of sympatry, there is a closer resemblance between species. Cohen (1976) found a single specimen of *L. pealei* with a GW/RW ratio below 2.4, and this specimen was from an area where both species occur. The possibility of

genetic introgression was considered by Cohen (1976), but currently there is no evidence of hybridization between any of the loliginid species.

The original intent of this study was to examine selected morphometric characters of potential value in differentiating the two common species of *Loligo* in the field. Juvenile and subadult squids comprise a substantial portion of the invertebrate biomass in the northern Gulf of Mexico, and difficulty in separating the species of *Loligo* has been a contributing factor in our lack of knowledge of this group. No single character or index enabled 100% separation of the species in the size classes of squid under study. Overlap was high in many of the measured characters and indices and precluded their use as reliable determinants of species. LaRoe (1967) and Cohen (1976) also found high overlap in measured characters and indices for the two species and suggested that more than one character or index had to be used to separate the species. In the present study, combinations of characters or indices associated with cartilaginous structures (FCL, GW, NCL, and RW) enabled greatest percent separation.

The single GW/RW ratio of 2.7 enabled correct identification of 91% of *L. pealei* and 100% of *L. plei*. This percent separation was similar to that achieved in the discriminant analysis for the GW/RW ratio. The most practical method for separation of the species in the field is use of the 2.7 GW/RW ratio in conjunction with the overall shape of the gladius, including the presence or absence of marginal ribs.

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Queen conch, *Strombus gigas*, in fished and unfished locations of the Bahamas: effects of a marine fishery reserve on adults, juveniles, and larval production

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Abstract.—Marine fishery reserves (MFR's) have been set aside in coastal areas throughout the world with the hope of reversing population decreases commonly observed in many marine resources. In this study, a comparison of population structure of the commercially important gastropod *Strombus gigas*, queen conch, was made between a fished area and an MFR in the Exuma Cays, central Bahamas. There were 31 times more adult conch on the shallow (<5 m) Great Bahama Bank in the MFR, and in a survey at 7 depth intervals (to 30 m) on the island shelf in the Exuma Sound, mean adult density was always higher in the MFR, by as much as 15 times. Shell length and lip-thickness measurements indicated that adults in the MFR migrate with age from bank nursery sites into deeper sound water, whereas those on the bank in the fished area were harvested before reaching water sufficiently deep to protect them from free-diving fishermen. Although sparsely distributed juveniles in shallow-water (<15 m) habitats of the sound were the primary source of adults in the fished area, large juvenile aggregations on the bank also contributed to the deep-water adult stock in the MFR.

Total larval densities in the MFR were frequently an order of magnitude higher than those found in the fished area, and densities of late-stage larvae were 4 to 17 times higher. Because the surface current along the Exuma Cays shelf flows to the northwest, late-stage larvae found inside the reserve must have been spawned outside the reserve; thus the high densities of juvenile and adult conch are the result of natural accumulation of larvae in the area, as well as the result of protection from fishing. Although the fate of larvae dispersed from the reserve is uncertain, it is likely that high numbers of reproductive stock and larvae in the reserve have a significant positive effect on populations in the northern Exuma Sound. Designs of reserves that consider ontogenetic requirements of the target species and strategic locations for larval production, import, export, and metapopulation dynamics will optimize fishery benefits for the many marine vertebrate and invertebrate species that possess pelagic larvae.

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In coastal areas throughout the world, tracts of coastline, reef, and banks known to be important spawning or nursery grounds for economically significant species are being set aside as marine fishery reserves (MFR's). Fishing in such areas is either controlled or prohibited to conserve or enhance production of selected species. Bohnsack (1990) listed 21 potential advantages of fishery reserves including important ecological benefits such as 1) protection of reproductive stocks and genetic diversity, 2) maintenance of the age and social structure of populations, 3) maintenance of areas of undisturbed critical habitat, 4) supplemental restocking of fished areas through emigration, and 5) provision for a larval source for recruitment to surrounding areas. Numerous other advantages of reserves relate to data collection and enforcement of regulations. Surveys of the literature (Roberts and Polunin, 1991; Dugan and Davis, 1993; Rowley, 1992) have yielded evidence that, in most cases, abundance and size of protected species increase within reserves, but there are few data to support the other predicted advantages (see also Roberts and Polunin, 1991; Polunin and Roberts, 1993).

Many fish and invertebrates produce planktonic larvae; therefore, in order to enhance fishery yields in the surrounding waters, an MFR must be located such that its larval production is exported to suitable habitats and to fished areas. Whether or not reserves are sources of recruitment for areas outside the protected waters is debated by environmental scientists, managers, and user groups. There are virtually no data to speak for or against the larval export benefit (Carr and Reed, 1993), although theoretical models incorporating the concepts of metapopulation dynamics indicate that MFR's should provide for larval recruitment to fished areas (Man et al., 1995). Similarly, there is little information on the emigration of

postsettlement fishes and invertebrates from MFR's into fished areas. A recent study (Rakitin and Kramer, 1996), designed to test for emigration of 24 fish taxa from the Barbados Marine Reserve, did not provide conclusive proof that the reserve allowed for exportation of fishes into the surrounding waters. Without solid data, managers will continue to face criticism from fishermen and other special interest groups that reserves are of no advantage to them or the environment.

In this study, a comparison of population structure of the commercially and culturally significant gastropod *Strombus gigas*, queen conch, was made between a fished area and an MFR in the Exuma Cays, an island chain in the central Bahamas (Fig. 1A). The fished area was near Lee Stocking Island,

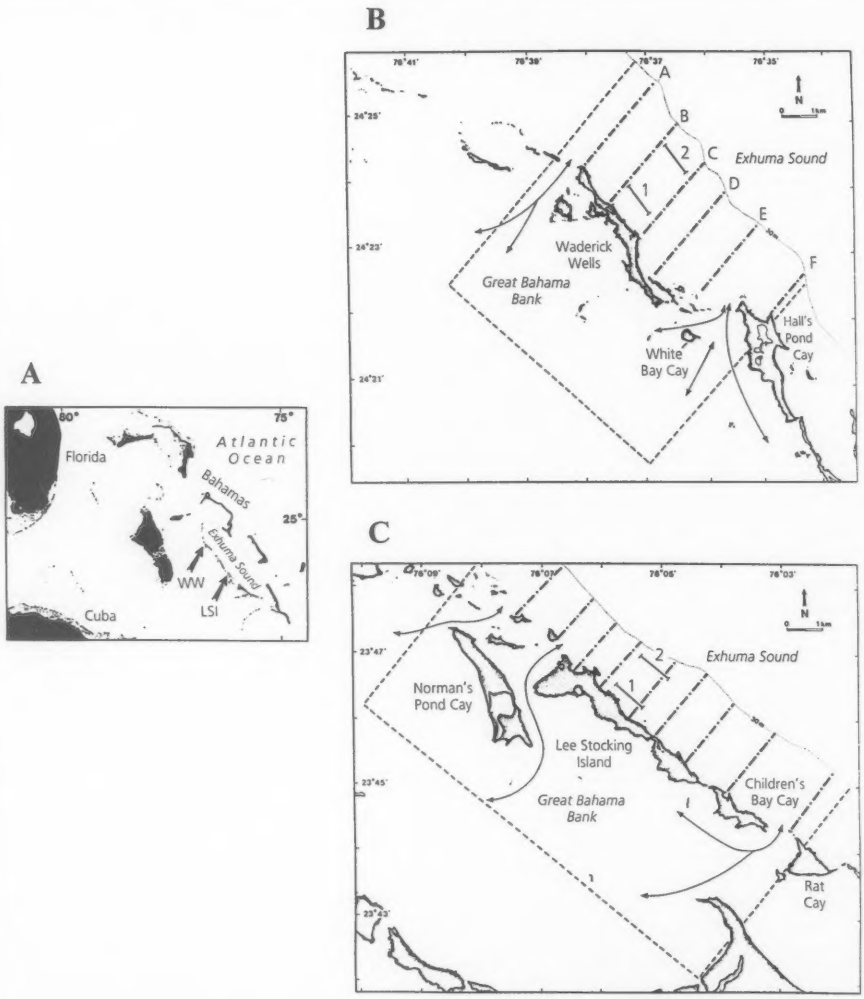

Figure 1

Maps showing 2 study sites in the Exuma Cays, central Bahamas (**A**). Waderick Wells (WW) (**B**) is located within the boundaries of a marine fishery reserve, but fishing is allowed near Lee Stocking Island (LSI) (**C**). In the detailed maps (B, C), dot-dash lines represent survey transects, solid lines with arrows indicate direction and extent of tidal flow, and solid lines labeled 1 and 2 show location of the inshore and offshore plankton tows. Area within the dashed lines and the 30-m isobath comprised the entire survey area.

at the southern end of the chain (Fig. 1C), and the MFR was 87 km north near Waderick Wells in the Exuma Cays Land and Sea Park (Fig. 1B). Our objectives were 1) to test the perceived benefits of an MFR by quantifying differences in densities of adults, juveniles, and larvae; 2) to consider physical-oceanographic mechanisms for such differences with respect to the open nature of the population; 3) to compare abundance patterns with data reported from other regions; 4) to determine sources of adult conch; and 5) to make management recommendations for a species that has been heavily exploited in many Caribbean locations.

Subject species

The natural history of the queen conch is relatively well known. The species is indigenous to subtropical and tropical waters of the western Atlantic from Bermuda and southern Florida to Venezuela and Trinidad (Abbott, 1974). Several egg masses, each containing ~400,000 eggs, are laid by females on clean sand during the summer season (Robertson, 1959; Stoner and Sandt, 1992). Larvae hatch in 3–5 d and live in the upper 5–10 m of the water column for 16–28 d, feeding on phytoplankton (Brownell, 1977; Davis et al., 1993; Stoner and Davis, in press, a). Vertical migration appears to be slight (Barile et al., 1994), and the larvae drift passively on near-surface currents (Stoner and Davis, in press, b). Genetic studies (Mitton et al., 1989; Campton et al., 1992) and analysis of queen conch larval life history and ocean currents in the Caribbean region (Davis et al., 1993) suggest that larvae can travel long distances to colonize seagrass nursery grounds where they settle and feed.

Young conch feed on seagrass detritus and algae (Randall, 1964; Stoner and Waite, 1991) and migrate into deeper water with age (Weil and Laughlin, 1984; Stoner and Schwarte, 1994). At 3.5–4 yr, queen conch reach sexual maturity, cease to grow in shell length, and begin to form the characteristic flared shell lip that thickens with age (Egan, 1985; Appeldoorn, 1988). Longevity is at least 6–7 yr (Berg, 1976) and may reach 26 yr in deep-water habitats (Coulston et al., 1987). Fishing regulations in the Bahamas prohibit the taking of any nonlipped (i.e. juvenile) queen conch and the use of SCUBA gear for any kind of fishing. A general lack of conch at depths >30 m has been attributed to low abundance of plant foods at such depths (Randall, 1964; Adams, 1970).

In 1990, the economic value of queen conch taken from the Caribbean region was estimated at $40 million (US) (Appeldoorn, 1994a). However, as a result of severe overfishing throughout its range (Berg and Olsen, 1989; Appeldoorn, 1994a), queen conch was considered commercially threatened worldwide in 1983 (Wells et al., 1983) and, in 1992, it was added to Appendix II of the Convention on International Trade in Endangered Species (CITES). Fisheries have been closed seasonally or for multiyear periods in areas of Venezuela, Colombia, Belize, Mexico, Cuba, and the U.S. Virgin Islands. Despite closure in Florida (since 1985) and Bermuda (since 1978), stock recovery has been slow (Appeldoorn, 1994a).

Methods

Study sites

The Exuma Cays island chain comprises more than 100 small islands that extend northwest to southeast in the central Bahamas, separating Exuma Sound from the Great Bahama Bank (Fig. 1). The bank is a shallow platform covered with sand and seagrass meadows. In the sound, the island shelf extends from land out 1–3 km to a steep shelf edge beginning at ~30 m depth. At both Lee Stocking Island (LSI) (Fig. 1C), where fishing is allowed, and at Waderick Wells (WW) (Fig. 1B), within an MFR, habitats in the depth range of 2.5–15 m include sand, coral rubble, algal-gorgonian hard-bottom, and seagrass. The hard-bottom is covered with the short turf of the green alga *Cladophoropsis* sp. in many subtidal locations. Beyond 15 m, the habitat is mostly sand and large coral ridges with some hard-bottom. Most of the rocky eastern shore of WW lacks beaches, and water depth close to shore is typically 2 m. At LSI, small sandy beaches lie in protected coves at certain locations between rocky headlands.

Water exchange between the bank and sound occurs through numerous passes that separate the islands, creating extensive tidal flow fields on the bank. At LSI (Fig. 1C), most queen conch reproductive activity occurs in the sound on the island shelf, where adults live in highest densities and juveniles are rare (Stoner and Schwarte, 1994). Larvae are carried through the tidal passes and settle onto the bank (Stoner et al., 1994; Stoner and Davis, in press, b) (Fig. 1, B and C). Discrete juvenile aggregations, with densities of 0.1–1.3 conch/m^2 (most >80 mm shell length), occur on the bank in the same general locations year after year (Wicklund et al., 1991; Stoner and Ray, 1993; Stoner et al., 1996) and may cover 5–600 ha. Most aggregations are located within 5 km of inlets on the Great Bahama Bank in beds of the seagrass *Thalassia testudinum* (Stoner et al., 1994).

The Exuma Cays Land and Sea Park, recognized as a protected area in 1958, extends 40 km along the

Exuma Cays and 13 km across the bank and sound to comprise 456 km^2. A full-time warden enforces park regulations, which strictly prohibit the collection of any plants or animals. This investigation was conducted near the island of Waderick Wells (Fig. 1B) where the park headquarters are located and fishing regulations are best enforced. The study area was well within the park boundaries, 10 km from the southern boundary of the park and 24 km from the northern boundary.

Adult surveys

For a comparison of fished and unfished areas, density surveys for adult queen conch were conducted on the bank and the island shelf, from beach to shelf edge, in the Exuma Sound near LSI between March and September 1991 (Stoner and Schwarte, 1994) and near WW in 1994 in this study. Annual surveys for adult conch conducted at selected sites off LSI, where fishing is allowed, showed little interannual variation in population size (Stoner and Sandt, 1992) and provide justification for the comparison of population densities in different years. Between 1988 and 1991, maximum variation from the mean population size was just 19%; the population was 4% above average in 1991. Adult densities at an important reproductive site at 18 m depth off LSI (Stoner and Sandt, 1992) differed only 8% between 1991 and 1994. Given the relative stability of adult conch populations at LSI and the long adult life (probably >20 years; Coulston et al., 1987), we concluded that surveys from WW and LSI could be compared. In addition, intrasite comparisons of conch density and age structure provided some of the most compelling evidence for the effects of fishing on the recruitment and population size. For direct comparison, survey methods for this study were similar to those used by Stoner and Schwarte (1994).

Near WW in the MFR, the bank survey area extended 7.5 km along the long axis of the island and 5 km southwest from the channels north and south (Fig. 1B), comprising 3,245 ha. Throughout this area, a snorkeler was towed behind a small boat for a total of 47 km while counting the number of adult conch within a 6-m-wide field of view and recording the locations in which adults were abundant. Tows were made along a total of 12 transects which ran perpendicular to WW. These transects started near the western shores of the primary islands and were less than 1 km apart. Latitude and longitude for the beginning and end of each transect were recorded with Global Positioning System (GPS). This resulted in direct observation of a surface area of 28.0 ha. Densities of adult conch were calculated for the transects, and the number of conch was extrapolated for the entire area.

To test the hypothesis that depth distribution of adults differed between the 2 sites, depth-stratified surveys for adult conch were conducted in Exuma Sound along 6 transects which ran perpendicular to WW. Transect A ran northeast from the north tip of WW, and transect F ran northeast from the north end of Hall's Pond Cay (Fig. 1B). Other transects were spaced as uniformly as possible between A and F, 1–2 km apart. Along each transect, estimates of conch density were made at 7 depth intervals: just off the beach (when present), 2.5–5 m, 5–10 m, 10–15 m, 15–20 m, 20–25 m, and 25–30 m. Within each interval, two SCUBA divers swam for 8–30 minutes, depending on depth, holding a line (8 m) between them and counting the number of adult conch that lay beneath the line. One diver carried a calibrated flow meter to calculate the distance traveled. To compensate for the potential influence of current on distance measured, the divers swam from the boat anchor into any discernible current and back, covering two parallel, nonoverlapping paths that normally ran parallel to the isobaths. Thirty-six dives were made during this shelf survey for adult conch density. The mean swim distance was 360 m (SD=6 m). Sampling effort was lowest for the 25–30 m interval because of diving limitations imposed by depth; however, the surface area of this deepest sampling zone was relatively small (Table 1). Again, results were directly comparable with Stoner and Schwarte (1994).

A bathymetric chart of the island shelf east of WW (to 45 m) was created from 250 points for which depth (corrected for tidal state) and position (determined with GPS) were recorded from a small boat. Computer-generated contour lines (1 m) were resolved with normal smoothing algorithms. Surface areas for each contour interval were calculated, and the mean density of conch found during the dive surveys was extrapolated to determine total number for each depth interval.

To examine age distribution and to evaluate potential migration patterns at WW, shell length and shell lip thickness were measured for at least 50 individuals at each depth interval on the shelf and for 213 individuals collected from several locations on the bank. Although young adults laid down lip material faster than older adults and although shells are subject to erosion, shell thickness at the lip provides a relative indication of conch age (Appeldoorn, 1988; Stoner and Sandt, 1992).

To test for differences in size and age distribution associated with depth, frequency distributions of shell length and shell lip-thickness data were analyzed by depth interval with the nonparametric Kolmogorov-Smirnov test. Several aspects of shell

Table 1

Comparison of the total abundance and density of adult queen conch, *Strombus gigas*, in the marine fishery reserve near Waderick Wells and in the fished area near Lee Stocking Island. Estimates for total abundance were extrapolated from bathymetric data and conch density surveys conducted in each habitat and range of depth. Values for adult density are mean ±SE; numbers in parentheses are the number of surveys at each depth.

	Marine fishery reserve			Fished area		
Habitat and depth (m)	Adults (no./ha)	Area (ha)	Total no. of conch	Adults (no./ha)	Area (ha)	Total no. of conch
Bank	53.6	3,245	174,080	1.7	3,997	6,816
Shelf						
0–2.5	0 ±0 (2)	158	0	0 ±0 (4)	161	0
2.5–5	34 ±22 (6)	200	6,871	2.2 ±1.7 (7)	198	444
5–10	49 ±18 (7)	1,035	51,138	7.2 ±4.1 (9)	465	3,353
10–15	270 ±85 (6)	375	101,187	60 ±47 (9)	429	25,800
15–20	104 ±58 (6)	193	20,113	88 ±32 (9)	454	39,902
20–25	148 ±72 (5)	136	20,108	18 ±9 (9)	320	5,843
25–30	122 ±70 (6)	71	8,635	0 ±0 (9)	151	0
Shelf total		2,167	208,053		2,178	75,342
Overall total		5,412	382,133		6,175	82,158

shape, including shell length, are induced by habitat characteristics of juvenile queen conch (Martín-Mora et al., 1995) and are conserved in adults (Stoner and Schwarte, 1994). For example, juvenile conch that develop in shallow seagrass beds of the bank cease to grow in shell length at a smaller size in comparison with conch developing on the shelf in Exuma Sound.

To test for differences in the density of adult queen conch among depth zones and between sites, 2-way analysis of variance (ANOVA) was performed on log-transformed data ($\log_{10}(n+1)$: there were numerous zeros in the data) in accordance with the guidelines of Day and Quinn (1989). Prior to analysis, variances were tested for heterogeneity with Cochran's test ($P>0.05$). The 2-way ANOVA was followed by Tukey's HSD multiple comparison test.

Because the comparison between the MFR near WW and the fished area near LSI constitutes an important aspect of this study, basic results from LSI (modified from Stoner and Schwarte, 1994) are reported in some figures and tables.

Juvenile surveys

To estimate abundance of juvenile queen conch at the two sites, we calculated the areal extent of juvenile aggregations at both WW and LSI. Aggregations of juvenile conch have abrupt boundaries and high densities are found adjacent to habitats without conch (Stoner and Ray, 1993). To estimate the size of aggregations in the study areas, divers were towed systematically over these areas to determine the boundaries within which density was ≥0.1 conch/m^2. Boundaries were marked with buoys, and buoy positions were determined with GPS. The potential error in positions measured with GPS is variable and can be as large as 150 m. However, when the points were plotted on a small-scale chart, they characterized accurately the shapes defined by the buoys in the field, and any error was uniform in direction and magnitude. Absolute position was not critical for the calculation of aggregation sizes. Surface areas of the aggregations were determined with the plots and a digitizing board. Surveys of juvenile queen conch have been conducted each summer since 1988 at LSI and were conducted in 1991 at WW. Juvenile conch were infrequently encountered on the island shelf; consequently, densities there were determined in conjunction with the adult survey.

At LSI, the juvenile surveys were concentrated in the flow field that begins just north of the island and runs south of Norman's Pond Cay onto the Great Bahama Bank and in the flow field that runs between Children's Bay Cay and Rat Cay (5 km) (Fig. 1C). Although most conch were associated with these tidal channels, the entire bank between Rat Cay and the north end of LSI was searched. At WW, the survey area comprised the flow field south of the island which extended onto the bank toward the south end of Hall's Pond Cay (6 km) and the surrounding bank areas (Fig.

1B). These particular tidal flow fields were emphasized because adults on the island shelf probably originated from nurseries in adjacent bank and shelf areas.

To compare juvenile conch abundance at WW and LSI, the percentage of the bank survey area occupied by juvenile aggregations was calculated (ha of aggregation/ha of bank area surveyed). Although this index provides only a crude comparison of juvenile abundance without quantitative data on animal density within the aggregations, our long experience with juvenile aggregations in the Exuma Sound has shown that aggregations rarely have <0.1 or >1.5 conch/m^2. General observations on densities were noted in our 1991 surveys at both sites.

Larval surveys

Surveys for queen conch larvae were conducted during the primary spawning season (June through August) at WW and LSI in order to provide information on the production of larvae in the two areas and to evaluate the supply of late-stage larvae. In 1993, samples were collected on 5 dates (12 June, 30 June, 15 July, 4 August, and 22 August) at each site over the island shelf at 1 inshore station (5-m isobath) and at 1 offshore station (20–30 m isobath) (Fig. 1, B–C). In 1994, samples were collected on 3 dates (22 June, 20 July, and 18 August) at only the offshore stations, where highest concentrations of adults occurred and where highest concentrations of late-stage larvae were collected in 1993. Simultaneous studies of spawning behavior at LSI and WW in 1995 showed that egg-laying is synchronous in the two areas (Stoner and Ray, unpubl. data).

Conical plankton nets (202-μm mesh, 0.5-m mouth diameter) were towed behind a 20-m vessel at 100 m/sec for replicated (n=2) 15-min tows. Because queen conch larvae are found in the upper water column during the day (Stoner and Davis, in press, a), nets were towed in the upper 1–2 m of the water column at inshore sites. At offshore sites, replicated 15-min tows were made for ~5 min at each of the following depths: 1 m, 2–3 m, and 5 m. The volume of water filtered on each tow was calculated from a calibrated flow meter (General Oceanics) secured in the mouth of the net. Samples were preserved in 5% formalin-seawater mixture. Strombid veligers were sorted from the plankton with a dissecting microscope and identified according to Davis et al. (1993). The number of queen conch veligers per 10 m^3 of water was calculated, and subsamples of veligers from each tow were measured for shell length. The veligers were classified as early-stage (≤500 μm), mid-size (500-900 μm), or late-stage (>900 μm). Late-stage larvae were metamorphically competent or nearly so.

Results

Adult surveys

Variation in density and abundance There were an estimated 208,500 adult conch in Exuma Sound near WW within the MFR survey area, which comprised 2,167 ha (Table 1). Two-way ANOVA of the 5 depth intervals from 2.5 to 25 m revealed significant differences both between the two different areas ($F_{1,63}$ =16.62, P<0.001) and among zones ($F_{4,63}$=3.87, P =0.007). The deepest interval (25–30 m) was excluded from analysis because adult conch were never observed at that depth in the fished area. Interaction between the two variables was not significant ($F_{4,63}$=1.48, P=0.218).

Mean adult density was always higher, by as much as 15 times, in the MFR than in the fished area for each depth interval (Table 1). Maximum mean density (270 conch/ha) occurred at 10–15 m in the MFR. This value was three times higher than the highest density observed in the fished area near LSI (88 conch/ha at 15–20 m) and was significantly higher than densities at all LSI depth intervals (Tukey test, P≤0.03) except 15–20 m (P=0.58).

Although nearly half the survey area in the MFR was 5–10 m deep (Table 1), adult densities were relatively low at depths <10 m (0–49 conch/ha) and high (≥104 conch/ ha) at all deeper intervals, even at greatest depth (122 conch/ ha at 25–30 m). No adults were observed at the two beach locations surveyed.

Variation in conch density within depth intervals was high and apparently related to island shelf structure. For example, density at 25–30 m was ≤6 conch/ha along transects D and E where the slope to the shelf edge increased sharply from 15 m, whereas density was 432 conch/ha farther north in transect C, where the slope to 30 m was more gradual.

The density of adult queen conch on the bank adjacent to WW and Hall's Pond Cay in the MFR (53.6 conch/ha) was 31 times higher than that in the fished area near LSI (1.71 conch/ha). Seventy-four percent of all adult conch encountered on the bank near WW were within 2 km of inlets; this general distribution pattern was also evident at LSI.

There was an estimated total of 174,100 adult queen conch on the bank in the entire MFR survey area (3,245 ha) (Table 1). This was 45.6% of the overall total for the shelf and bank. In the fished area, there were only 6,816 adults in the bank area surveyed (3,997 ha), and this number comprised a relatively small portion of the overall total for the site (8.3%). Most adult conch in the fished area (>87%) were found in depths >10 m, whereas only 39% of adult conch in the MFR were in depths >10 m.

Shell structure Pairwise Kolmogorov-Smirnov tests showed differences in frequency distributions of shell length in the MFR between adult conch on the bank and those at each depth interval ($P \leq 0.002$ in all cases) except 2.5–5 m ($P=0.14$). Adult conch from the sound, always ≥150 mm, tended to be longer than those from the bank (Fig. 2). The length mode for sound conch ranged from 180–189 mm (at 5–10 m and 10–15 m) to 210–219 mm (at 15–20 m and at 25–30 m, where the largest individual [265 mm] was found). Conch at the deepest interval were relatively large, and mean shell length increased 18 mm between the 10–15 m and 25–30 m intervals. A bimodal distribution was observed in the three deepest intervals, with a low frequency of 200–209 mm conch in all cases. Mean shell length for all conch from the sound was 202 mm (SD=21 mm, $n=524$), compared with 188 mm (SD=20 mm, $n=213$) for conch on the bank. An intersite comparison showed significant differences in frequency distributions of shell length between the MFR and the fished area for conch living at each depth interval but not for those on the bank (Fig. 2). Adult conch from the shelf in the fished area had longer shells than those from the shelf in the MFR.

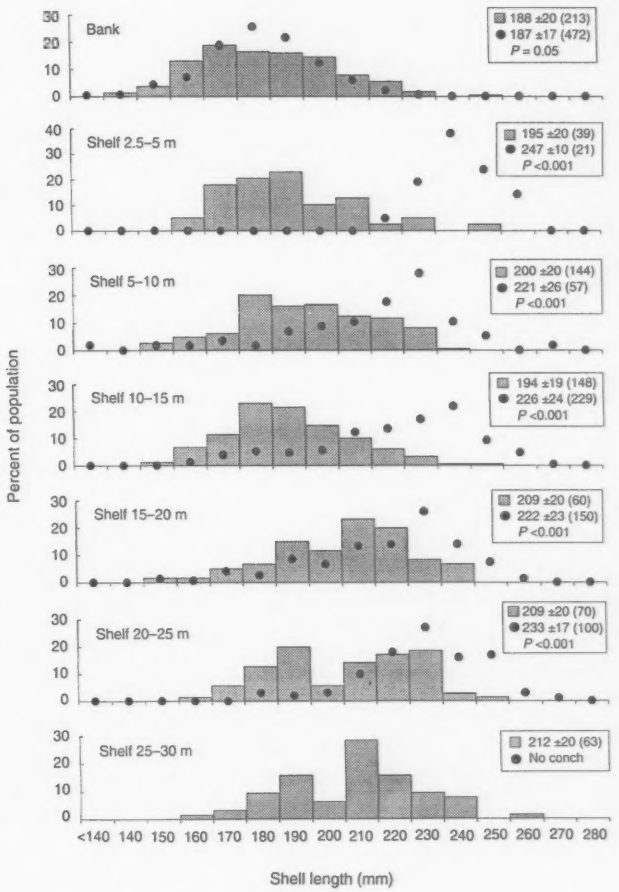

Figure 2

Frequency distribution of shell length of adult conch on the bank and at 6 depth intervals in Exuma Sound on the island shelf near WW in the marine fishery reserve (columns) and in the fished area near LSI (points). Each value on the x-axis represents a range of sizes starting with the lower end of the size interval (e.g. 150–159 mm). Mean shell length (±SD) and sample size in parentheses are also given for each distribution. Values for LSI are adapted from Stoner and Schwarte (1994). *P*-values are for intersite comparisons (Kolmogorov-Smirnov tests).

Pairwise Kolmogorov-Smirnov tests also showed differences in frequency distributions of shell lip thickness in the MFR between adult conch on the bank and those at each depth interval ($P<0.001$ in all cases) because those on the bank had relatively thin shell lips. All bank adults had shell lips ≤28 mm thick, and 31% were ≤8 mm (Fig. 3). Lip thickness values were >16 mm for most adults in the sound, and <5% of the conch at each of the three depth intervals to 15 m had lip thickness ≤8 mm. Beyond 15 m no thin-lipped conch were measured. Mean lip thickness for all conch from the sound was 24 mm (SD=7 mm, $n=524$), compared with 12 mm (SD=6 mm, $n=213$) on the bank.

An intersite comparison showed significant differences in frequency distributions of shell lip thickness for conch living on the bank and at each depth interval ($P \leq 0.001$ in all cases) except for those at 5–10 m ($P=0.08$) (Fig. 3). Compared with conch in the MFR, conch in the fished area tended to have thinner lips in shallow water (bank, and sound <5 m) and thicker lips in deeper water.

Juvenile surveys

Juvenile conch were never observed at depths >15 m in the Exuma Sound at either study area, and they were infrequently observed (mean <6/ha) in shallower water in the MFR (Fig. 4). Highest density of

juveniles in the sound (33.3 juveniles/ha) occurred in the MFR at 5–10 m, but the standard deviation for this depth interval was more than twice the mean (all other densities were 0, except 1 at 5.1 juveniles/ha). In contrast with adults, intersite differences for juvenile densities in Exuma Sound were not significant (Student's t-test, $P>0.2$ for 2.5–5 m, 5–10 m, and 10–15 m).

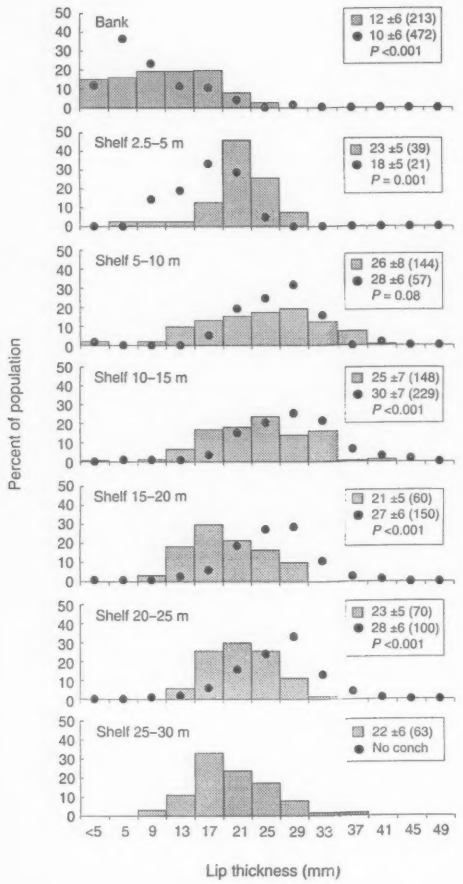

Figure 3

Frequency distribution of shell lip thickness of adult conch on the bank and at 6 depth intervals in Exuma Sound on the island shelf near WW in the marine fishery reserve (columns) and in the fished area near LSI (points). Each value on the x-axis represents a range of sizes starting with the lower end of the size interval (e.g. 5–8). Mean lip thickness (±SD) and sample sizes in parentheses are also given for each distribution. Values for LSI are adapted from Stoner and Schwarte (1994). P-values are for intersite comparisons (Kolmogorov-Smirnov tests).

The majority of juvenile conch at both sites were found on the Great Bahama Bank. On the bank in the fished area, interannual variation in the surface area occupied by juvenile aggregations was high, ranging from 8 to 44 ha in the flow field north of LSI and from 2 to 87 ha in the Children's Bay Cay flow field (Table 2). In the MFR in 1991, juveniles occupied 125 ha. Although data for the MFR are available for only 1 yr, the surface area was nearly twice a large as the average surface area occupied in two flow fields over 6 yr in the fished area. In the MFR, juvenile aggregations covered 3.84% of the bank area surveyed, compared with a mean value of 1.62% in the fished area.

Larval surveys

Densities of queen conch larvae were consistently higher in the MFR near WW than in the fished area near LSI. In 50 plankton tows made at the two sites between 1993 and 1994, densities in the fished area were always <6 larvae/10 m^3 and typically near 1–2 larvae/10 m^3 (Table 3). Densities in the MFR were frequently an order of magnitude higher, reaching a maximum of 55 larvae/10 m^3 in July 1994. Intrasite differences were most notable in the MFR on 22 August 1993 when the offshore station had 184 times the density of veligers as the inshore station. However, results were variable, and during both June cruises in 1993, the inshore station at the MFR had

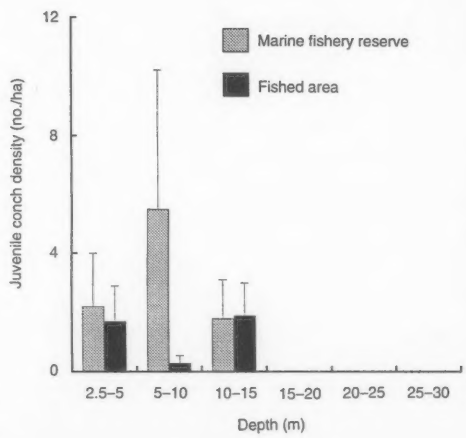

Figure 4

Juvenile conch density at 6 depth intervals in Exuma Sound on the island shelf at the fished area near LSI (Stoner and Schwarte, 1994) and at the marine fishery reserve near WW (this study). Values are mean (+SE).

higher mean larval densities than the offshore station (Table 3).

Early-stage larvae (≤500 μm SL) represented the most abundant size class in collections made at both areas (>90%) (Table 4). Late-stage larvae (≥900 μm SL) were always present in the MFR, except on 22 June 1994, and always occurred at higher densities in the MFR than in the fished area. The highest observed density was 1.9 late-stage larvae/10 m^3 on 4 August 1993. Late-stages were also more abundant offshore than inshore at both sites.

Discussion

Comparisons with earlier investigations

Although direct comparisons of LSI/WW density data with data from other studies are made difficult because of different sampling strategies, incomplete data in some reports, and failures to distinguish between adult and juvenile densities, a review of the literature suggests high regional variability in adult queen conch densities, ranging over three orders of

Table 2

Surface area occupied by juvenile queen conch in two tidal flow fields, one originating north of Lee Stocking Island (LSI), and the second originating between Rat Cay and Children's Bay Cay (CBC) (see Fig. 1C). Surface areas for LSI and CBC were standardized to percent of bank surface area occupied by juvenile aggregations.

	Surface area (ha)			
Year	LSI	CBC	Total	% of bank
1989	31.7	32.2	63.9	1.60
1990	14.5	7.4	21.9	0.55
1991	19.4	1.7	21.1	0.52
1992	8.3	51.7	60.0	1.50
1993	42.2	86.8	129.0	3.23
1994	44.3	49.2	93.5	2.34
Mean	26.7	38.2	64.9	1.62
SD	14.9	31.6	41.8	1.05

Table 3

Larval densities (no. 10/m^3) (mean ±SD) in a marine fishery reserve near Waderick Wells (WW) and in a fished area near Lee Stocking Island (LSI). Samples were collected inshore and offshore for 5 days in 1993 and offshore for 3 days in 1994. *P*- and *t*-values are from Student's *t*-test using pooled variances when data were homogeneous (Cochran's test, $P>0.05$) and from separate variances when data were not ($0.01<P<0.05$).

1993	12 Jun	30 Jun	15 Jul	4 Aug	22 Aug
Inshore					
WW	50.0 ±5.1	43.6 ±5.4	0.65 ±0.33	4.42 ±0.52	0.22 ±0.21
LSI	0.52 ±0.21	2.70 ±0.45	0.63 ±0.44	no data	1.58 ±0.77
t	–13.83	–10.66	–0.06		2.41
P	0.005	0.009	0.96		0.14
Offshore					
WW	36.3 ±2.7	7.26 ±1.12	0.91 ±0.62	1.87 ±0.19	40.4 ±15.4
LSI	0.62 ±0.19	1.00 ±0.10	1.22 ±0.09	0.74 ±0.44	0.43 ±0.24
t	–18.42	–7.85	0.71	–3.33	–3.66
P	0.003	0.02	0.55	0.08	0.17
1994	22 Jun	20 Jul	18 Aug		
Offshore					
WW	27.8 ±5.09	54.7 ±9.35	0.98 ±0.18		
LSI	5.94 ±1.44	0.25 ±0.23	0.06 ±0.08		
t	–5.86	–8.23	–6.73		
P	0.03	0.08	0.02		

Table 4

Densities of queen conch veligers (no. /10 m^3) in three size classes in a marine fishery reserve near Waderick Wells and in a fished area near Lee Stocking Island. Samples were collected inshore and offshore in 1993 and offshore in 1994. Values are mean ±SD; the numbers in parentheses are the number of sampling dates for each site.

	Early-stage (<500 μm)	Mid-size (500–900 μm)	Late-stage (>900 μm)
1993			
Marine fishery reserve			
Inshore	19.7 ±24.9 (5)	0.037 ±0.073 (5)	0.042 ±0.060 (5)
Offshore	15.9 ±18.8 (5)	0.646 ±0.874 (5)	0.768 ±0.701 (5)
Fished Area			
Inshore	1.25 ±1.07 (4)	0.093 ±0.134 (4)	0.011 ±0.008 (4)
Offshore	0.740 ±0.348 (5)	0.018 ±0.017 (5)	0.045 ±0.058 (5)
1994			
Marine fishery reserve			
Offshore	27.4 ±27.0 (3)	0.322 ±0.206 (3)	0.110 ±0.111 (3)
Fished Area			
Offshore	2.05 ±3.33 (3)	0 ±0 (3)	0.029 ±0.025 (3)

magnitude (Table 5). Mean values in the MFR near WW for each depth interval were always ≥34/ha, well above those reported for Bermuda, Florida, Puerto Rico, and the U.S. Virgin Islands. Densities in the MFR in depths >10 m were comparable to those observed before 1984 at Cabo Cruz, Cuba, in the Turks and Caicos Islands, and at a fished area of Venezuela. Only two other studies quantified adult conch densities by depth (Table 6). In Puerto Rico, maximum adult density occurred at 20–25 m, but the value was only 0.05 adults/ha (Torres Rosado, 1987), three orders of magnitude lower than that for our MFR, and two orders of magnitude lower than that at our fished area near LSI. In the U.S. Virgin Islands, adult density was maximum (17.1 adults/ha) at 18–24 m (Friedlander et al., 1994), and nearly identical to densities (18.3 adults/ha) observed in 20–25 m in our fished area.

Highest densities reported in the literature were observed >20 years ago in Cuba and >10 years ago in Venezuela. The highest single density estimate in our study (568 adults/ha) represented only 30–36% of the highest densities reported for Diego Perez, Cuba (1,582/ha), and for a fishery reserve at Islas Los Roques in Venezuela (1,886/ha) (Table 5). This protected area in Venezuela was subsequently depleted of adult conch through illegal fishing (Rodríquez and Posada, 1994), and declines in population density throughout the Caribbean are well documented (Appeldoorn, 1994a). Densities of conch in the Exuma Cays are now among the highest in the region.

Low numbers of adults found in shallow water have been attributed directly to fishing off the Turks and Caicos Islands (Hesse, 1979), Venezuela (Weil and Laughlin, 1984), Puerto Rico (Torres Rosado, 1987), the U.S. Virgin Islands (Friedlander et al., 1994), and the Bahamas (Stoner and Schwarte, 1994). In this investigation there were >31 times the number of adult conch on the bank in the MFR compared with the number in the fished area. Because any adult conch living in water <10 m deep near LSI can be collected easily by abundant free-diving fishermen, we also attribute density differences between our sites at least partly to fishing, although other explanations are also plausible (see below).

Densities of queen conch larvae have been reported in only two published studies. Our estimates of density near WW, commonly >30 veligers/10 m^3, were much higher than these studies. The highest density from a cruise in the eastern Caribbean in 1988 was only 1.2 veligers/10 m^3 (mid- and late-stages) near the Grenadines (Posada and Appeldoorn, 1994), and the highest value found near Puerto Rico in 1993 was only 0.68 veligers/10 m^3 (Appeldoorn and Rodriquez[1]). The highest single value recorded for a site outside the Exuma Sound was 2.0 veligers/10 m^3 (including newly hatched larvae) in the Florida Keys in 1994, with all other values one or two orders of magnitude lower (Stoner et al., in press; Stoner and Mehta, unpubl. data). High larval densities in the Exuma Cays, particularly in the MFR, appear to be directly associated with abundance of spawning stocks.

[1] Appeldoorn, R. S., and L. Rodriquez. 1995. Department of Marine Sciences, University of Puerto Rico, P.O. Box 908, Lajas, Puerto Rico 00667. Unpubl. data.

Table 5

Adult queen conch densities reported throughout the Caribbean and arranged by decreasing latitude.

Location	Density (no/ha)	Depth (m)	Survey date	Reference	Survey methods
Bermuda	0.52	0–20	1988	Berg et al. (1992a)	Towed-diver transects
Florida Keys, United States	0.50	0–25	1987–1988	Berg et al. (1992b)	Stratified towed-diver transects
Bahamas			1983–1984	Smith and van Nierop[1]	Swim transects
Little Bahama Bank	28.50	0–18			
Great Bahama Bank	20.79	0–18			
Cuba			1972–1974	Alcolado (1976)	Swim transects
Diego Perez	1582	3–4			
Cabo Cruz	130	0–5			
Turks and Caicos Islands	255	0–4	1974–1975	Hesse (1979)	Swim transects
Puerto Rico, United States	2.62	0–30	1985–1986	Torres Rosado (1987)	Swim transects
Virgin Islands, United States		—	1981	Wood and Olsen (1983)	Sled transects
St. Thomas	9.7				
St. Croix	7.6				
Virgin Islands, United States			1990	Friedlander et al. (1994)	Scooter transects
St. Thomas	11.79	5–30			
St. John	12.64	5–30			
Los Roques, Venezuela			1981–1983	Weil and Laughlin (1984)	Fixed quadrats
Fished	160[2]	1–4			
Unfished	1886[2]	1–18			

[1] Smith, G. B., and M. van Nierop. 1984. Distribution, abundance, and potential yield of shallow-water fishery resources of the Little and Great Bahama Banks. UNDP/FAO Fish. Dev. Proj. BHA/82/002, p. 1–78.
[2] Assuming conch >210 mm in shell length were adults (Laughlin and Weil, 1983).

Distribution processes in the Exuma Cays

In terms of both density and extrapolated total numbers there were more adult conch in the MFR near WW than in the fished area near LSI. The two sites were similar in terms of habitat, and they lie relatively close together in the same oceanographic basin, yet there were density differences, most notably in the shallow bank waters. We recognize that no unreplicated comparison of two field sites can provide indisputable proof that an MFR is advantageous to a stock unless the analysis includes long time series or data before and after closure of a fishing area, or both (Stewart-Oaten et al., 1986; Osenberg et al., 1994; Underwood, 1994). Unfortunately we know of no biological data for the Exuma Cays Land and Sea Park collected before the fishing closure. This is a common problem associated with studies of MFR's (see Roberts and Polunin, 1991), and future studies should use control sites and replication in both time and space for definitive answers regarding the impact of closing fisheries in reserve areas. On the other hand, it is not surprising when stocks of exploited species increase in closed areas. A more important issue may be whether or not the reserves contribute to long-term conservation of species or whether or not they preserve or enhance stocks in the surrounding waters. Answers to such questions require data

Table 6

Adult queen conch densities reported for two locations in the Caribbean by depth interval. Data for Puerto Rico were collected in 1985–86 (Torres Rosado, 1987) and data for the United States Virgin Islands were collected in 1990 (Friedlander et al., 1994). See Table 1 for comparison with the Exuma Cays sites.

Puerto Rico		Virgin Islands	
Depth (m)	Density (no/ha)	Depth (m)	Density (no/ha)
0–5	0	0–6	5.2
5–10	0.04	6–12	4.2
10–15	0.035	12–18	17.1
15–20	0.035	18–24	10.9
20–25	0.05	24–30	11.0
25–30	0.023		

on mechanistic issues such as reproductive output, recruitment dynamics, and larval import and export. Our data on adult shell size and age, juveniles, and larval size and abundance make this analysis unique and allow considerable insight into distribution mechanisms in the Exuma Cays. An understanding of such mechanisms is critical for making effective management policies.

Site-specific differences in shell size and shape described for queen conch (Stoner and Schwarte, 1994; Martín-Mora et al., 1995) are useful in explaining adult recruitment patterns at WW and LSI. Juveniles in the shelf environment of Exuma Sound grow rapidly, produce shells that are long and slender, and reach sexual maturity (hence terminal length) at a larger size than conch developing on the Great Bahama Bank. On the basis of shell size and shape, low numbers of adults on the bank and near inlets, and high fishing pressure, Stoner and Schwarte (1994) concluded that little migration occurred between bank and sound at LSI and that small numbers of juveniles in shallow regions of the sound were the primary source of deep-water reproductive stock. Adults on the bank were mostly young (i.e. thin-lipped), and most were removed by fishing before they could migrate offshore to the primary reproductive grounds in the deeper shelf environment.

Adults on the bank in the MFR near WW had a length-frequency distribution virtually identical to those on the bank at LSI (i.e. small adults). However, unlike the LSI shelf where large adults dominated the population, adult length-frequency in the shelf environment of WW was bimodal. The smaller WW adults originated on the bank and were able to migrate to deeper shelf waters in the absence of fishing. Therefore, although there was only one primary source of adults for the sound population at LSI, there were two sources at WW, and migration from the unfished bank provides at least a partial explanation for higher densities and the bimodal distribution observed on the adjacent Exuma Sound shelf. Although, in some areas, fishing may result in removal of large individuals and in artificial selection for small conch (Appeldoorn, 1994b), this does not appear to be a problem near LSI, where adults were relatively large.

On the basis of shell lip thickness, it appears that conch were removed from the bank near LSI at an early age, whereas older, thick-lipped conch accumulated on the bank in the MFR near WW. The reverse was evident in deep shelf waters where the average age of conch was higher at LSI than at WW. It is possible that harvesting of young adults from shallow bank and shelf waters near LSI has reduced recruitment to the deep-water spawning population. It has been assumed that, by allowing fishermen to collect conch only by free-diving, a deep-water refuge is secured for conch spawning stock. Although this is true in general, virtually all juveniles and first-year adults in the Exuma Cays live in shallow (<15 m) water and all are available to free-diving fishermen until after reaching adulthood. Protection of habitat used as a migratory pathway is critical in the management of conch stocks.

Patterns of abundance for queen conch juveniles and larvae suggest that differences in recruitment processes, in addition to fishing pressures, may affect differences in the numbers of adult conch between the two study sites. In 1991, juvenile aggregations in the MFR were an order of magnitude larger than those in the fished area, where the aggregations were relatively small in all six annual surveys. The large juvenile aggregations in the MFR can be explained by relatively high densities of competent larvae arriving at the site. In 1993, the mean concentration of late-stage larvae at the offshore shelf stations at the MFR was 17 times higher than the concentration in the fished area. In 1994, the difference was approximately fourfold. The supply of larvae to the MFR nurseries appears to be much higher than the supply to nurseries in the fished area.

Differences in larval supply to a site are affected by three primary processes—production, survival, and transport. Virtually nothing is known about the predators of queen conch larvae or about the survival of queen conch in the plankton. There is little doubt, however, that site differences in larval production, demonstrated by the density of early-stage larvae, reflect local spawning stock size and density. In terms of transport, near-surface flow along the Exuma Cays shelf is to the northwest at LSI, at WW, and at a station midway between the two sites. From June through September 1993, the current on the shelf at WW flowed to the northwest at 1.6–3.4 cm/s (1.4–2.9 km/day (Hickey[2]). Given a larval life of 16–28 d (Davis et al., 1993), late-stage queen conch larvae arriving in the MFR near WW must originate well to the south, and their high densities most likely reflect a natural accumulation of larvae produced by spawning stocks all along the Exuma Cays. This abundance of recruits must also contribute to high densities of juveniles and adults observed in the MFR. Larvae of a closely related, but unfished strombid, *Strombus costatus*, were also highly concentrated in the MFR in 1994 (Stoner, unpubl. data). We conclude, therefore, that the high density of adult conch at WW results not only from reduced fishing

[2] Hickey, B. A. 1995. School of Oceanography, Univ. Washington, Seattle, WA 98195. Unpubl. data.

pressure but also from natural accumulation of larvae. Furthermore, given the surrounding current patterns, the reserve is probably not large enough to hold a self-sustaining conch population; conch at WW are derived from up-stream spawning stocks located outside the reserve. With a northwest current along the Exuma Cays shelf, an MFR located farther to the south might actually allow better downstream conservation of queen conch. However, exact transport distances are unknown, and calculations are complicated by the potential effects of numerous tidal passes and plumes. Because preservation of external sources of larvae will be critical to the maintenance of populations within any park, managers establishing all such reserves must consider the broad metapopulation context (Carr and Reed, 1993; Man et al., 1995).

It is likely that the high densities of larvae exported from the Exuma Park on the northwest current represent a significant recruitment source for conch populations in the northern Exuma Sound. Very large aggregations of juvenile conch (>600 ha) were measured in the northern Exuma Sound near the Schooner Cays in 1993 (Stoner, unpubl. data). These populations appear to have increased since the establishment of the Exuma Cays Land and Sea Park (Higgs[3]). Future modeling of larval transport will be particularly valuable in estimating the actual significance of enhanced larval production in this and other marine fishery reserves. Although the significance of larval export is difficult to prove experimentally (Dugan and Davis, 1993), the value of reserves located upstream may be especially high.

Clearly, the Exuma Cays Land and Sea Park is large enough to protect a large reproductive stock of queen conch in an undisturbed habitat where physical oceanographic features concentrate competent larvae and export them to downstream nurseries and fishing grounds. Because of the potential fishery value of exported larvae, a good understanding of the strategic locations of reserves and of the general oceanographic conditions within the dispersal range of the larvae is necessary. Our observations provide support that fishery reserves can indeed enhance fishery populations in the downstream direction through export of larvae, although only if the sources of larvae for the reserves are maintained. Furthermore, reserves need to incorporate design features that protect habitats required by each life stage. Legal prohibition of the use of SCUBA gear prevents immediate depletion of adult queen conch because those individuals that survive the migration to deep-water constitute an unfished deep-water reproductive stock, even outside a reserve. However, every young adult is vulnerable, and multiple well-placed reserves that protect the tidal inlets, which serve as pathways between nurseries and important reproductive grounds on the shelf, could be particularly valuable. Reserve designs that consider ontogenetic requirements of the target species and strategic locations for larval production, import, export, and metapopulation dynamics will optimize fishery benefits for the many marine vertebrate and invertebrate species that possess pelagic larvae.

[3] Higgs, C. 1994. Department of Fisheries, Ministry of Agriculture, Trade, and Industry, P.O. Box N3028, Nassau, Bahamas. Personal commun.

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Transferrin polymorphism in coho salmon, *Oncorhynchus kisutch*, and its application to genetic stock identification

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Abstract.—The blood protein transferrin is an important source for identifying genetic variation in coho salmon, *Oncorhynchus kisutch*, with starch gel electrophoresis. We present new data for transferrin allele frequencies for 48 samples of coho salmon collected at 34 different locations from Oregon to southern British Columbia. To analyze transferrin allele frequencies from a larger geographic area, data from various sources were compiled for 135 samples from sites from California to southern British Columbia. In a statistical analysis of temporal variation within locations, 26 of 63 pairwise comparisons (41%) showed significant differences between samples ($P<0.05$). An analysis of variance revealed significant between-locale variability and no significant within-locale variability due to whether or not the brood years of the samples were three years apart. Relative gene diversity values were 22.3% between geographic regions, 2.1% between stocks within geographic regions, 3.1% between temporal comparisons, and 72.5% for within-sample variation. Total genetic diversity (H_T) was 0.586, and the average genetic diversity within populations (H_s) equaled 0.425. The samples showed genetic variation that was related to geographic location. Applications of transferrin data to genetic stock identification are discussed in relation to these results.

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The iron binding protein, transferrin (Tf), is a highly polymorphic locus in coho salmon, *Oncorhynchus kisutch*, that exhibits allelic frequency differences between populations (Utter et al., 1970; Hjort and Schreck, 1982; Olin, 1984; Bartley et al., 1992). The transferrin locus is a potentially valuable addition to the set of polymorphic loci currently used for genetic stock identification (GSI) of coho salmon (Milner, 1993). In the past, one drawback of including transferrin in multilocus GSI surveys was the necessity of acquiring a serum sample to resolve allelic variation. However, transferrin allele frequencies can now be obtained from heart tissue (Van Doornik et al., 1995), therefore it is feasible to incorporate variation at this locus into GSI analyses involving coho salmon.

This study was conducted as part of an ongoing research effort to develop a geographically extensive baseline of allele frequencies for coho salmon. Our objectives are to increase the number of polymorphic loci for which allele-frequency data are obtainable, to verify the genetic basis of previously documented and new allelic variation, and to expand the geographic range of our baseline data set. Given adequate geographic coverage and genetic differences among major contributing stocks, allele-frequency data can be used for stock identification of mixed stock fisheries (Milner et al., 1985; Milner, 1993).

The objective of this paper is to examine the potential of transferrin for use in genetic stock identification of coho salmon. Specifically, we 1) report new transferrin allele frequencies for 48 samples collected from 34 coho salmon stocks, 2) compile allele-frequency data for transferrin data from other sources to compare allele frequencies over a larger geographic area, 3) analyze the temporal stability of transferrin allele frequencies, and 4) examine levels and patterns of variation between samples using gene diversity and genetic identity analyses.

Materials and methods

Blood or tissue samples, or both, were collected, as described by Van Doornik et al. (1995), for 48 coho

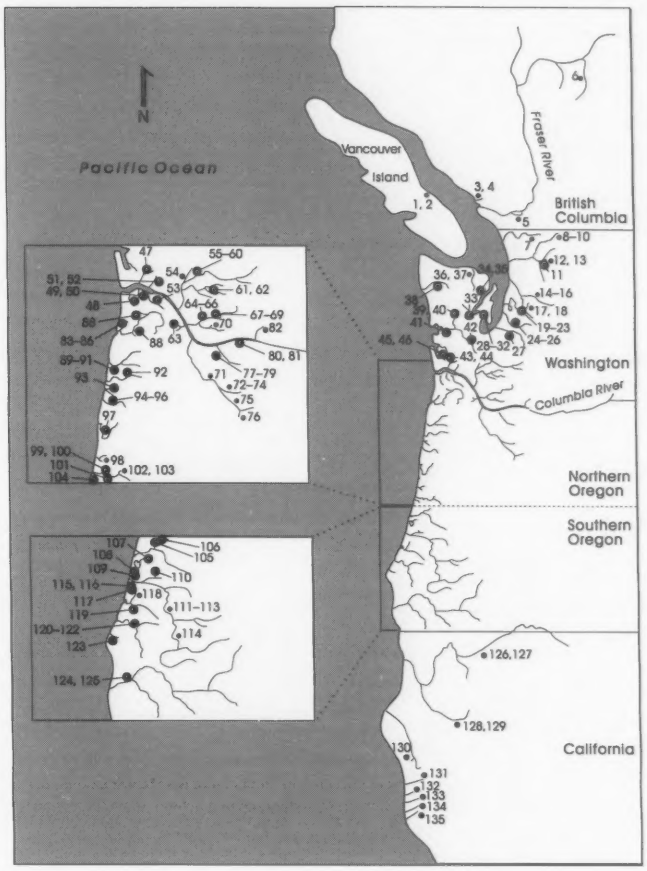

Figure 1

Locations of samples. Numbers refer to sample names identified in Table 1.

salmon samples from 34 locations in northern Oregon (north of Cape Perpetua), the Columbia River, Washington coastal streams, and Puget Sound, Washington (Fig. 1). Starch gel electrophoresis was conducted as described by Aebersold et al. (1987) and Van Doornik et al. (1995).

Observed genotype frequencies were compared with expected Hardy-Weinberg proportions with a chi-square goodness-of-fit test for the 48 samples for which genotype-frequency data were available.

Allele frequencies were compiled from other studies that included 30 or more fish per sample for the transferrin locus to create a data set of 135 samples (Table 1). The log-likelihood ratio statistic (G-test) (Sokal and Rohlf, 1969) was used to compare allele frequencies of these samples that were taken in different years at the same locale. In these analyses, G-tests were performed for each polymorphic locus and the results were summed over all loci to yield an overall G-value and a standardized G-value (G/df). To test for significant differences between samples, an analysis of variance (ANOVA) of arc sine square-root transformed allele frequencies, for n–1 alleles, was conducted with SYSTAT statistical software (SYSTAT, 1992). Genetic diversity was partitioned into components defined by regions, samples, and within-sample (temporal variation) according to the method described by Chakraborty (1980) by using the BIOSYS-1 computer program (Swofford and Selander, 1981).

Genetic similarities among samples were estimated with Nei's (1978) unbiased genetic identity and projected as a dendrogram with the unweighted pair-group method with arithmetic averaging (UPGMA) (Sneath and Sokal, 1973) (with BIOSYS-1). Genetic similarities were also analyzed by using

a principal components analysis of the correlation matrix with NTSYS software (Rohlf, 1994).

A noteworthy characteristic of coho salmon populations south of Alaska is their unique propensity to return to spawn at three years of age (Sandercock, 1991). We classified samples from the same locale as "on cycle" if the brood years were three years apart and as "off cycle" when otherwise. We tested for a significant effect of brood-year cycle within a locale on allele frequencies by nesting the brood-year cycle within-locale in the above mentioned ANOVA.

Results

Four alleles were observed with relative mobilities of 106, 103, 100, and 97. The **106* allele was observed at only three locations (Cowlitz, Lewis, and Trinity rivers) at a low frequency ($P<0.03$). Frequencies of the other alleles varied considerably among samples: $0.116 \leq P \leq 1.000$ for the **103* allele, $0.000 \leq P \leq 0.535$ for the **100* allele, and $0.000 \leq P \leq 0.764$ for the **97* allele. Allele frequencies for the 48 new samples analyzed in our laboratory are included in Table 1 (identified as "NMFS").

Of the 48 samples, 3 (6.3%) deviated from expected Hardy-Weinberg proportions: Nehalem Hatchery, brood year 1982 ($P=0.022$); Bonneville Hatchery, brood year 1989 ($P=0.008$); and Minter Creek Hatchery, brood year 1990 ($P=0.039$). Although the total number of significant tests ($n=3$) was only slightly greater than the number expected by chance alone ($n=2.4$), we have no reason to reject the assumptions that the samples represented panmictic populations and the genetic model used to interpret the observed allozyme patterns was correct. Data from an inheritance study have confirmed that the transferrin alleles segregate according to expected Mendelian segregation proportions (Van Doornik, unpubl. data).

Transferrin data compiled from nine sources in addition to those collected for this study are shown in Table 1. The total data set included 135 samples from sites ranging from California to southern British Columbia (Fig. 1). Sample sites were grouped into the following eight geographic regions: Vancouver Island, mainland British Columbia, Puget Sound, coastal Washington, Columbia River, northern Oregon (north of Cape Perpetua), southern Oregon, and California.

Sixty-three pairwise, *G*-tests were made by comparing allele frequencies of samples from the same location but from different brood years. A total of 41% ($n=26$) of the temporal comparisons were statistically significant ($P<0.05$). Despite this substantial temporal variability, the ANOVA indicated significant between-sample variation ($F=21.1$, df=89, $P=0$). (The rare **106* allele was pooled with the **103* allele frequencies for this analysis.) The contribution of brood-year cycle within sample locations to the overall genetic variation was not statistically significant for the **100* allele ($F=2.1$, df=24, $P=0.06$) and the **103* allele ($F=0.9$, df=24, $P=0.60$).

The gene diversity analysis indicated that most of the genetic diversity was found within locations (72.5%). The other components of relative gene diversity were 22.3% between geographic regions, 2.1% between stocks within a geographic region, and 3.1% between temporal comparisons. Relative gene diversity (G_{st}) equaled 27.5%. Total genetic diversity (H_T) was 0.586, and the mean genetic diversity within populations (H_s) equaled 0.425.

A dendrogram of Nei's genetic identity (I) for the compiled data for 135 samples revealed three major clusters at I=0.900 that followed regional geographic patterns (Fig. 2). All samples from Vancouver Island ($n=2$), the Washington coast ($n=8$), Puget Sound ($n=32$), and northern Oregon ($n=22$) formed cluster 1. Cluster 1 is distinguished by samples with moderate frequencies of the **103* ($0.080<P<0.501$) and **97* ($0.250<P<0.77$) alleles. The 21 samples from southern Oregon appeared in all three clusters. Samples from Marlow Creek, Five Mile Creek, Elk Creek, Coos River, North Fork Siuslaw River, and two Umpqua River stock samples (brood year 1981, 1992) also grouped in cluster 1; cluster 3 contained samples from the Rogue River ($n=2$) and Morton Creek; and the remaining 11 southern Oregon samples formed the sole members of cluster 2. Cluster 2 contained samples with relatively high frequencies of the **100* allele ($0.356 <P<0.540$). All of the California ($n=10$), Columbia River ($n=36$), and mainland British Columbia ($n=4$) samples grouped together in cluster 3. Cluster 3 consisted of samples with high frequencies of the **103* allele ($0.640<P \leq 1.000$).

The principal components analysis yielded results identical to those from Nei's genetic identity values, and therefore, are not included here.

Discussion

The geographical pattern of genetic variability shown by these data supports several conclusions regarding the genetic population structure of some of these stocks. Results from cluster analysis of the total data set (Fig. 2) indicated that samples from large river systems (Fraser River, Columbia River, Rogue River, and Klamath River) are genetically similar to each other despite the geographical distances separating them. Several studies have shown that coho salmon from small coastal rivers differ from those from large

inland river systems. For example, Hjort and Schreck (1982) examined electrophoretic, morphological, and life-history characteristics of coho salmon in Washington, Oregon, and California. They found, in general, stocks from large rivers (Columbia River, Rogue River, and Klamath River) were more similar to each other than to stocks from smaller rivers. Taylor and McPhail (1985) also found significant differences in body shape

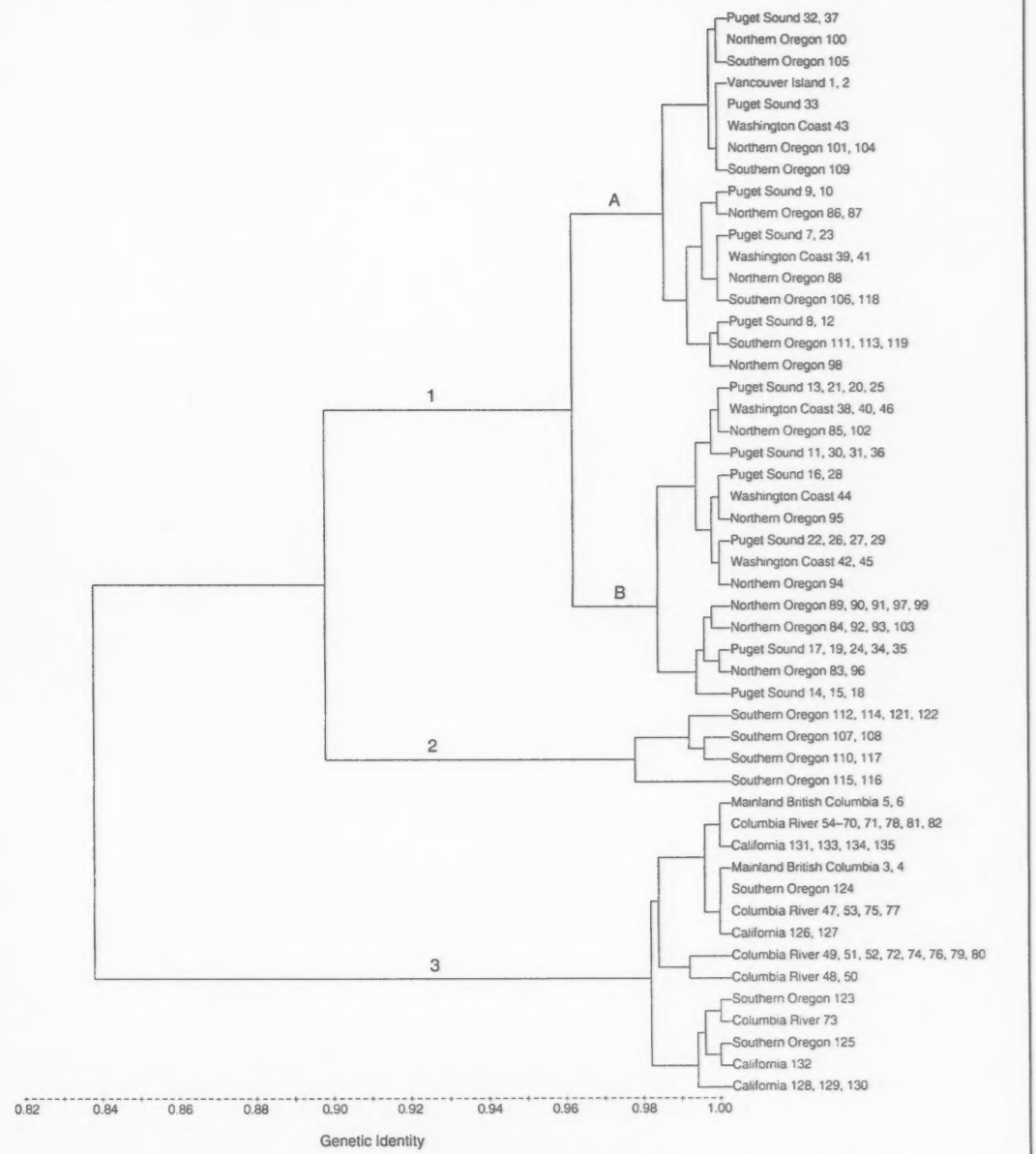

Figure 2

Dendrogram for compilation of 135 samples created with UPGMA clustering of Nei's identity values (Nei, 1978). Numbers refer to sample names identified in Table 1.

Table 1

Sample information, map codes, and allele frequencies for 135 samples of coho salmon, *Oncorhynchus kisutch*, from 81 locations.

Sample number	Name	Sample size	Brood year	Allele frequencies *103	*100	*97	*106	Source
1	Qualicum Hatchery	30	1971	0.367	0.333	0.300	0.000	Utter[1]
2	Qualicum Stock at Capillano Hatchery	91	1976	0.352	0.313	0.335	0.000	Utter[1]
3	Capillano Hatchery	45	1971	0.822	0.089	0.089	0.000	Utter[1]
4	Capillano Hatchery	85	1976	0.847	0.011	0.142	0.000	Utter[1]
5	Hope River, Fraser River	35	1972	1.000	0.000	0.000	0.000	May and Utter[2]
6	Coldwater River at Spius Hatchery	76	1985	0.961	0.039	0.000	0.000	NMFS[3]
7	North Fork Nooksack River	51	1974	0.402	0.196	0.402	0.000	May (1975)
8	Baker River	79	1989	0.544	0.146	0.310	0.000	NMFS[3]
9	Baker River at Skagit Hatchery	87	1989	0.466	0.098	0.437	0.000	NMFS[3]
10	Baker River at Skagit Hatchery	60	1991	0.483	0.125	0.392	0.000	NMFS[3]
11	Skagit Hatchery	40	1974	0.262	0.250	0.488	0.000	May (1975)
12	Clark River at Skagit Hatchery	79	1989	0.544	0.120	0.335	0.000	NMFS[3]
13	Clark River at Skagit Hatchery	57	1991	0.254	0.211	0.535	0.000	NMFS[3]
14	Skykomish River Hatchery	67	1971	0.149	0.104	0.747	0.000	Utter et al. (1973)
15	Skykomish River Hatchery	125	1972	0.116	0.120	0.764	0.000	May and Utter[2]
16	Skykomish River Hatchery	66	1974	0.356	0.053	0.591	0.000	May (1975)
17	Deep Creek, Snoqualmie River	30	1974	0.267	0.117	0.616	0.000	May (1975)
18	Harris Creek, Snoqualmie River	30	1974	0.083	0.167	0.750	0.000	May (1975)
19	Issaquah Hatchery	50	1968	0.220	0.160	0.620	0.000	Utter et al. (1970)
20	Issaquah Hatchery	100	1971	0.235	0.170	0.595	0.000	Utter et al. (1973)
21	Issaquah Hatchery	180	1972	0.278	0.172	0.550	0.000	May and Utter[2]
22	Issaquah Hatchery	88	1973	0.307	0.165	0.528	0.000	May (1975)
23	Issaquah Hatchery	80	1974	0.331	0.162	0.507	0.000	May (1975)
24	Green River Hatchery	54	1968	0.222	0.139	0.639	0.000	Utter et al. (1970)
25	Green River Hatchery	87	1971	0.282	0.155	0.563	0.000	Utter et al. (1973)
26	Green River Hatchery	58	1974	0.353	0.190	0.457	0.000	May (1975)
27	Puyallup Hatchery	60	1974	0.358	0.150	0.492	0.000	May (1975)
28	Minter Creek Hatchery	50	1968	0.410	0.060	0.530	0.000	Utter et al. (1970)
29	Minter Creek Hatchery	84	1971	0.357	0.140	0.503	0.000	Utter et al. (1973)
30	Minter Creek Hatchery	175	1972	0.289	0.200	0.510	0.000	May and Utter[2]
31	Minter Creek Hatchery	79	1974	0.215	0.259	0.526	0.000	May (1975)
32	Minter Creek Hatchery	34	1990	0.338	0.235	0.426	0.000	NMFS[3]
33	George Adams Hatchery	88	1974	0.295	0.341	0.364	0.000	May (1975)
34	Quilcene River Hatchery	60	1968	0.200	0.125	0.675	0.000	Utter et al. (1970)
35	Quilcene River Hatchery	60	1971	0.200	0.125	0.675	0.000	Utter et al. (1973)
36	Dungeness River Hatchery	47	1971	0.287	0.266	0.447	0.000	Utter et al. (1973)
37	Dungeness River Hatchery	80	1985	0.331	0.313	0.356	0.000	NMFS[3]
38	Soleduck River Hatchery	50	1971	0.190	0.220	0.590	0.000	Utter et al. (1973)
39	Simpson Hatchery	127	1972	0.378	0.224	0.398	0.000	May and Utter[2]
40	Simpson Hatchery	40	1992	0.275	0.212	0.513	0.000	NMFS[3]
41	Chehalis Hatchery	51	1971	0.373	0.236	0.411	0.000	Utter et al. (1973)
42	Newaukem River at Green River Hatchery	42	1974	0.393	0.119	0.488	0.000	May (1975)
43	Willapa River Hatchery	50	1971	0.280	0.350	0.370	0.000	Utter et al. (1973)
44	Willapa River Hatchery	37	1990	0.338	0.054	0.608	0.000	NMFS[3]
45	Nemah Hatchery	50	1971	0.300	0.180	0.520	0.000	Utter et al. (1973)
46	Nemah Hatchery	74	1974	0.223	0.216	0.561	0.000	May (1975)
47	Grays River Hatchery	39	1989	0.872	0.038	0.090	0.000	NMFS[3]
48	Klaskanine Hatchery	85	1990	0.653	0.029	0.318	0.000	NMFS[3]
49	Big Creek Hatchery	77	1989	0.812	0.013	0.175	0.000	NMFS[3]
50	Big Creek Hatchery	100	1990	0.675	0.015	0.310	0.000	NMFS[3]
51	Elokomin Hatchery	50	1968	0.800	0.000	0.200	0.000	Utter et al. (1970)
52	Elokomin Hatchery	98	1971	0.786	0.000	0.214	0.000	Utter et al. (1973)
53	Clatskanie River	31	1989	0.855	0.097	0.048	0.000	NMFS[3]
54	Lacamas River at Cowlitz Hatchery	32	1974	0.906	0.063	0.031	0.000	May (1975)

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Table 1 (continued)

Sample number	Name	Sample size	Brood year	Allele frequencies *103	*100	*97	*106	Source
55	Cowlitz Hatchery, Early	70	1989	0.908	0.021	0.043	0.028	NMFS[3]
56	Cowlitz Hatchery, Late	39	1989	0.961	0.013	0.000	0.026	NMFS[3]
57	Cowlitz Hatchery	50	1971	1.000	0.000	0.000	0.000	Utter et al. (1973)
58	Cowlitz Hatchery	38	1983	0.974	0.013	0.013	0.000	Gall[4]
59	Cowlitz Hatchery	52	1983	0.894	0.077	0.190	0.010	Gall[4]
60	Cowlitz Hatchery	100	1990	0.955	0.025	0.020	0.000	NMFS[3]
61	Toutle River Hatchery	50	1968	1.000	0.000	0.000	0.000	Utter et al. (1970)
62	Toutle River Hatchery	100	1971	0.980	0.000	0.020	0.000	Utter et al. (1973)
63	Scappoose Creek	40	1989	0.938	0.038	0.025	0.000	NMFS[3]
64	Lewis Hatchery, Early	78	1989	0.923	0.071	0.006	0.000	NMFS[3]
65	Lewis Hatchery, Late	79	1989	0.962	0.025	0.000	0.013	NMFS[3]
66	Lewis Hatchery, Late	86	1990	0.913	0.029	0.058	0.000	NMFS[3]
67	Speelyai Creek Hatchery	50	1968	0.990	0.000	0.010	0.000	Utter et al. (1970)
68	Speelyai Creek Hatchery	99	1971	1.000	0.000	0.000	0.000	Utter et al. (1973)
69	Speelyai Creek Hatchery	96	1990	0.938	0.010	0.052	0.000	NMFS[3]
70	Rock Creek, East Fork Lewis River	31	1974	0.935	0.000	0.065	0.000	May (1975)
71	Clackamas River	30	1989	1.000	0.000	0.000	0.000	NMFS[3]
72	Eagle Creek at Clackamas Hatchery	50	1983	0.800	0.010	0.190	0.000	Gall[4]
73	Eagle Creek Hatchery	75	1989	0.713	0.167	0.120	0.000	NMFS[3]
74	Eagle Creek Hatchery	96	1990	0.792	0.005	0.203	0.000	NMFS[3]
75	North Fork Clackamas Dam	40	1990	0.900	0.013	0.087	0.000	NMFS[3]
76	Fish Creek, Clackamas River	42	1983	0.774	0.000	0.226	0.000	Gall[4]
77	Sandy River Hatchery	50	1983	0.880	0.000	0.120	0.000	Gall[4]
78	Sandy River Hatchery	75	1989	0.947	0.013	0.040	0.000	NMFS[3]
79	Sandy River Hatchery	100	1990	0.770	0.055	0.175	0.000	NMFS[3]
80	Bonneville Hatchery	49	1983	0.806	0.031	0.163	0.000	Gall[4]
81	Bonneville Hatchery	79	1989	0.949	0.013	0.038	0.000	NMFS[3]
82	Willard Hatchery	80	1989	0.944	0.038	0.019	0.000	NMFS[3]
83	Nehalem River at Nehalem Hatchery	87	1981	0.213	0.109	0.678	0.000	Olin (1984)
84	Nehalem River at Nehalem Hatchery	79	1992	0.209	0.019	0.772	0.000	NMFS[3]
85	Nehalem Hatchery	84	1982	0.226	0.185	0.589	0.000	NMFS[3]
86	Nehalem Hatchery	73	1990	0.445	0.130	0.425	0.000	NMFS[3]
87	Cronin Creek, Nehalem River	36	1981	0.486	0.028	0.486	0.000	Olin (1984)
88	Fishhawk Creek at Nehalem Hatchery	63	1981	0.413	0.198	0.389	0.000	Olin (1984)
89	Trask Hatchery	79	1981	0.285	0.025	0.690	0.000	Olin (1984)
90	Trask Hatchery	117	1991	0.265	0.021	0.714	0.000	NMFS[3]
91	Trask River at Trask Hatchery	79	1992	0.291	0.032	0.677	0.000	NMFS[3]
92	Bogus Creek, Nestucca River	79	1983	0.215	0.017	0.766	0.000	Gall[4]
93	Hawk Creek, Neskowin River	47	1981	0.181	0.053	0.766	0.000	Olin (1984)
94	Salmon River Hatchery	71	1981	0.317	0.141	0.542	0.000	Olin (1984)
95	Salmon River Hatchery	86	1982	0.343	0.116	0.541	0.000	NMFS[3]
96	Salmon River at Salmon River Hatchery	80	1992	0.237	0.094	0.669	0.000	NMFS[3]
97	Siletz River at Salmon River Hatchery	77	1992	0.227	0.026	0.747	0.000	NMFS[3]
98	Beaver Creek	46	1981	0.500	0.250	0.250	0.000	Olin (1984)
99	Alsea River at Fall Creek Hatchery	85	1981	0.259	0.041	0.700	0.000	Olin (1984)
100	Alsea River at Fall Creek Hatchery	44	1992	0.386	0.273	0.341	0.000	NMFS[3]
101	Meadow Creek, Alsea River	41	1981	0.341	0.354	0.305	0.000	Olin (1984)
102	Fall Creek at Fall Creek Hatchery	50	1983	0.240	0.170	0.590	0.000	Gall[4]
103	Fall Creek at Fall Creek Hatchery	68	1992	0.176	0.059	0.765	0.000	NMFS[3]
104	Yachats River	35	1981	0.271	0.314	0.415	0.000	Olin (1984)
105	North Fork Siuslaw River	70	1983	0.371	0.236	0.393	0.000	Gall[4]
106	Elk Creek, Siuslaw River	47	1981	0.457	0.181	0.362	0.000	Olin (1984)
107	Maple Creek	41	1983	0.427	0.402	0.171	0.000	Gall[4]
108	Tahkenitch Lake at Fall Creek Hatchery	77	1992	0.377	0.409	0.214	0.000	NMFS[3]
109	Five Mile Creek	41	1981	0.329	0.341	0.330	0.000	Olin (1984)
110	Johnson Creek	49	1981	0.400	0.500	0.100	0.000	Olin (1984)

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Table 1 (continued)

Sample number	Name	Sample size	Brood year	Allele frequencies *103	*100	*97	*106	Source
111	Umpqua River at Rock Creek Hatchery	74	1981	0.478	0.179	0.343	0.000	Olin (1984)
112	Umpqua River at Rock Creek Hatchery	50	1983	0.570	0.410	0.020	0.000	Gall[4]
113	Umpqua River at Rock Creek Hatchery	69	1992	0.522	0.188	0.290	0.000	NMFS[3]
114	South Fork Umpqua River at Butte Falls Hatchery	70	1992	0.529	0.357	0.114	0.000	NMFS[3]
115	Eel Lake at Butte Falls Hatchery	120	1981	0.280	0.535	0.185	0.000	Olin (1984)
116	Eel Lake at Butte Falls Hatchery	63	1992	0.286	0.492	0.222	0.000	NMFS[3]
117	Tenmile Lake	50	1981	0.466	0.489	0.045	0.000	Olin (1984)
118	Marlow Creek	50	1981	0.375	0.182	0.443	0.000	Olin (1984)
119	Coos River at Cole River Hatchery	65	1992	0.546	0.169	0.285	0.000	NMFS[3]
120	Coquille River	84	1983	0.280	0.535	0.185	0.000	Gall[4]
121	Coquille River at Butte Falls Hatchery	57	1992	0.509	0.412	0.079	0.000	NMFS[3]
122	Coquille River at Butte Falls Hatchery	73	1981	0.570	0.410	0.020	0.000	Olin (1984)
123	Morton Creek	48	1981	0.643	0.204	0.153	0.000	Olin (1984)
124	Rogue River	65	1983	0.869	0.077	0.054	0.000	Gall[4]
125	Rogue River at Cole River Hatchery	57	1992	0.702	0.281	0.018	0.000	NMFS[3]
126	Klamath River at Irongate Hatchery	92	1981	0.852	0.031	0.117	0.000	Olin (1984)
127	Klamath River at Irongate Hatchery	81	1983	0.852	0.031	0.117	0.000	Gall[4]
128	Trinity River Hatchery	83	1983	0.813	0.181	0.000	0.006	Gall[4]
129	Trinity River Hatchery	111	1985	0.831	0.164	0.000	0.005	Bartley (1987)
130	Huckleberry Creek, South Fork Eel River	52	1985	0.837	0.163	0.000	0.000	Bartley (1987)
131	Pudding Creek	47	1985	0.914	0.057	0.029	0.000	Bartley (1987)
132	Caspar Creek	82	1985	0.730	0.230	0.040	0.000	Bartley (1987)
133	Russian Gulch	31	1985	1.000	0.000	0.000	0.000	Bartley (1987)
134	Little River	51	1985	0.929	0.071	0.000	0.000	Bartley (1987)
135	Albion River	30	1985	0.944	0.056	0.000	0.000	Bartley (1987)

[1] Utter, F. M. 1979. Memorandum dated January 19, 1979 to Dr. Keith Sandercock, Canadian Dep. of the Environment, Vancouver, B.C. Subject: Transferrin frequencies of coho salmon from Qualicum and Capillano Hatcheries, 3 p.
[2] May, B., and F. M. Utter. 1974. Biochemical genetic variation of the genus *Oncorhynchus* in Pacific Northwest populations: a progress report and program summary, 12 p. Available: Washington Dep. Fisheries, P.O. Box 43151, Olympia, WA 98504–3151.
[3] Samples analyzed in our laboratory.
[4] Gall, G. A. E. 1991. Allele frequencies of selected stocks of California, coastal Oregon, and Columbia River coho salmon, 59 p. Available: Dep. Animal Sci., Univ. California, Davis, CA 95616-8521.

of juvenile coho salmon between fish from coastal rivers and those from large inland river systems. They concluded that these differences are coastwide and are at least partially genetically determined.

It is possible that there is some selective pressure on the transferrin alleles occurring in large rivers, because all the samples from the Fraser, Columbia, Rogue, and Klamath rivers have high frequencies of the **103* allele, and low frequencies of the **97* allele.

Samples from California clustered with Columbia River samples. California stocks may have been affected by imported stocks: most of California's hatchery stocks originated from eggs imported from Oregon (Bartley et al., 1992), primarily from hatcheries on the Columbia River (Brown et al., 1994).

In other areas, however, stocks appear to follow a regional pattern of genetic differences, despite transfers of fish between geographical areas. For example, the Bonneville and Klaskanine Hatcheries on the Columbia River have received hatchery stocks from northern and southern Oregon (Oregon Dep. Fish and Wildlife[1]), yet still remain most similar genetically to other Columbia River samples (Fig. 2). Again, this could be due to selective factors unique to a given area.

Our findings are similar to results from related genetic studies of coho salmon. Noting allele frequencies at 26 enzyme loci, Wehrhahn and Powell (1987) also found significant differences between samples from Vancouver Island and the southern coastal region of mainland British Columbia. In a study of mitochondrial DNA variation in coho salmon from Oregon, Currens and Farnsworth[2] found that Colum-

[1] Oregon Department of Fish and Wildlife. 1991. Lower Columbia River coho salmon, evaluation of stock status, causes of decline, and critical habitat—Part 2. Report to ESA Administrative Record, 43 p., plus appendices. Available: Oregon Dep. Fish Wildl., P.O. Box 59, Portland, OR 97207.

[2] Currens, K. P., and D. Farnsworth. 1993. Mitochondrial DNA variation in Oregon coho salmon. Report to Oregon Department of Fish and Wildlife, 12 p. Available: Oregon Dep. Fish Wildl., P.O. Box 59, Portland, OR 97207.

bia River samples clustered separately from northern Oregon coastal samples. However, the two southern Oregon coastal samples that they examined (Rogue River and Coquille River) clustered with the Columbia River samples, rather than with samples from the Oregon coast. This result is similar to ours, except that the Coquille River did not cluster with Columbia River samples in our analysis.

Another important discovery was the relatively high level of temporal variation for transferrin allele frequencies. Accurate stock identification from allele-frequency data requires that allele frequencies remain relatively stable over time. Because most coho salmon south of Alaska return to spawn at 3 years of age (Sandercock, 1991), it is possible that allele frequencies for a particular stock could show marked differences between brood years. Waples and Teel (1990) found that for salmon populations where 90% of a brood year returned to spawn in the same year, the probability of finding a significant test for temporal differences increased dramatically.

Our test for temporal allele stability assumed there was no influx of nonnative fish into the gene pool; however, it is unlikely that this assumption was valid. All comparisons were made between samples obtained from hatcheries, and many of these hatcheries have imported and released fish that were not native to the hatchery location. For example, from 1952 to 1991, 20.2% of the coho salmon released at the Minter Creek Hatchery were not native to Minter Creek (Washington Dep. Fish and Wildlife[3]).

Another assumption that we made when testing temporal stability was that no natural selection occurred. Previous studies have found some evidence that transferrin alleles are influenced by natural selection. Suzumoto et al. (1977) observed that fish that have the **97* transferrin allele are less susceptible to bacterial kidney disease (BKD). Pratschner (1978) found that the **103/*103* phenotype had greater resistance to furunculosis, whereas the **97/*97* phenotype was most resistant to vibriosis. A study by McIntyre and Johnson (1977) indicated that fish with a **103/*103* phenotype had a faster growth rate than those with a **103/*97* phenotype, but the escapement rate for the two different phenotypes was equal. However, results of a study by Winter et al. (1980) conflicted with both Suzumoto et al. (1977) and Pratschner (1978). Their results indicated that only certain stocks show a genetically influenced resistance to BKD, furunculosis, and vibriosis. They concluded that "the importance of transferrin genotypes in resistance to disease is stock specific." The extent to which these factors affect transferrin allele frequencies and how they relate to GSI analyses are uncertain. If certain alleles are being selected for, according to location-specific factors, then allele frequencies could be more stable over time for a given location, even after nonnative stocks are introduced into an area. However, if selection factor(s) were to change, allele frequencies would change significantly over time, which would help to explain the large percentage of significant temporal comparisons that we found.

We found at least as much temporal variation between samples analyzed in our own lab as we did between samples analyzed in two different laboratories. Therefore, we ruled out the possibility that temporal variation was due to differing techniques or to differing interpretations of data, or both, in two different laboratories.

These results suggest that before the transferrin locus is used in GSI analysis, temporal variation of allele frequencies between brood years will need to be considered. However, temporal variation does not necessarily preclude the use of the transferrin locus in GSI analysis. In a study of temporal variation in lake trout, *Salvelinus namaycush*, Grewe et al. (1994) found that although there were significant differences in allele frequencies between year classes, the accuracy of their mixed-stock contribution estimates was not substantially affected. Waples (1990) suggested that to obtain maximum precision of estimates, temporally spaced samples should be pooled, unless the temporal differences are too large to be attributable to sampling error and to genetic drift. Of course, if the baseline data include only the brood years known to be contributing to the mixed-stock, temporal variation will not be a problem.

The mean heterozygosity value we calculated (0.425) was indicative of a high level of heterozygosity for the transferrin locus. This was one of the highest mean heterozygosity values we have observed for any polymorphic locus in coho salmon (Van Doornik, unpubl. data). It is also one of the highest mean heterozygosity values in comparison with other studies of salmonids. For example, the highest mean heterozygosity found by Wehrhahn and Powell (1987) in their study of 26 coho salmon loci from 95 sites in British Columbia was 0.0099 for the locus *LDH-B2** (transferrin was not included in this study). The largest mean heterozygosity value, in a study of 25 loci of 86 populations of chinook salmon, was 0.420 for the locus *PGK-2** (Utter et al., 1989).

As shown by the results from the ANOVA, there were significant differences between samples. The relative gene diversity values showed that there was

[3] Washington Department of Fish and Wildlife. 1994. Historical releases of juvenile salmon into Washington waters, coho salmon. Available: Washington Dep. Fish Wildl., 600 Capitol Way N., Olympia, WA 98501-1091. (Interactive database).

a high degree of genetic differentiation between samples from different geographic regions (22.3%). However, the level of differentiation between samples within regions was actually less than the level of temporal variation. This could be due to the extensive number of stock transfers within regions that have taken place for coho salmon. Therefore, we concluded that although the transferrin locus may be used to discriminate between samples from different geographic regions, caution must be used when attempting to use this locus to discriminate between samples from within a region.

It is important to realize that these results and conclusions are based on data from only one locus. Accurate GSI procedures rely upon baseline data from many polymorphic loci. Our current protocol for obtaining baseline genetic data includes using more than 60 loci that have been shown to be polymorphic for coho salmon. A large baseline of genetic information, from potential source populations and from enough loci with significant allele-frequency differences between stocks, to identify the contributing stocks is generally required for GSI methods to be successful (Milner et al., 1985).

Our results provide further evidence that identifiable regional genetic differences can be detected among coho salmon populations. GSI investigations of coho salmon will be more precise when data from the transferrin locus is used in conjunction with allozyme data and perhaps DNA-type variation (Park et al., 1993). As these data show, the transferrin locus exhibits significant allele-frequency differences between stocks from different geographical areas and has the potential to increase the discriminating power of GSI analyses for coho salmon.

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A catch-length analysis for crab populations*

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Abstract.—A catch-length model was constructed to estimate abundance of crab populations for which no survey data are available. The model incorporates stochastic growth by length and gradual recruitment over length and assumes constant catchability. Required data include catch by length and shell condition, fishing effort, growth increment per molt by length, and annual natural mortality rate. Model application to red king crab populations in Bristol Bay and off Kodiak Island, Alaska, generally provides accurate estimates of trends of relative population abundances. The accuracy of absolute abundance estimates depends on knowledge of natural mortality. The model provided a good fit to the catch by length and shell condition for both populations. In comparison to population abundances estimated directly from surveys, the catch-length model performed best with instantaneous natural mortality set equal to 0.4 and with fishing effort and catch-length/shell composition weighted equally in the calculation of residual sum of squares.

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Molting is one of the most important biological differences between crabs and fishes. The hard structure of crabs is replaced during molting, which makes direct ageing of crabs extremely difficult. The molting process of an individual crab is short, normally a few days, resulting in punctuated growth. Molting frequency of red king crab (RKC, *Paralithodes camtschaticus*) depends on body size and varies over time (Balsiger, 1974). Thus, ability to age crabs indirectly by conventional length-frequency analysis is questionable. Without age information, a conventional catch-age analysis cannot be applied to crab populations.

An alternative to a catch-age analysis is a catch-length analysis which combines information on fishing effort, catch at length, growth, and natural mortality to estimate recruitment and population abundance. During the past decade, much progress has been made to improve catch-length analysis. Lai and Gallucci (1988) examined the effects of parameter variation on length-cohort analysis, Fournier and Doonan (1987) developed a length-based production model, and Schnute (1987) derived a general size-structured population model. Sullivan et al. (1990) constructed a catch-length analysis which incorporates stochastic growth and separates recruitment into year and length components. However, most catch-length analyses were developed or applied to fish populations. Some size-frequency analyses have been conducted for decapods (Jones, 1979; Caddy, 1987; Fogarty and Idoine, 1988), but to our knowledge, few catch-length analyses have been applied to crabs.

Some commercially important crab populations are assessed annually by trawl surveys, and population abundances can be directly estimated from assessment data. Previously, we developed a length-based population model using such crab survey data to estimate population parameters and to improve abundance estimates (Zheng et al., 1995). However, for many crab populations the only usable data available are fishing effort and catch at length. Thus, a logical choice is to estimate abundance of crab populations using these data.

Our purpose in this study is to develop a catch-length analysis to estimate population size for unsurveyed crab populations. We modified the length-based population model developed by Zheng et al. (1995) for application to fishing effort and catch-at-length data that are routinely collected from many

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crab pot fisheries. The model incorporates stochastic growth, in which individual crabs molt with an annual molting probability and gradual recruitment over length. We applied our catch-length analysis to RKC populations in Bristol Bay and off Kodiak Island, Alaska. Bristol Bay RKC have supported one of the most valuable fisheries in the United States. The Kodiak RKC fishery was also very valuable before it collapsed in the early 1980's, and the population has failed to recover since then. We selected these stocks because both populations have been intensively studied during the last three decades and because data are available to estimate biological parameters such as growth and mortality. Moreover, the availability of annual trawl or pot survey data allowed us to compare population abundances estimated from the catch-length analysis and from surveys to determine the reliability of the catch-length analytical methods that we developed.

Methods

Data requirement

Data required for the model include annual length-frequency of commercial catches by shell condition, total annual catch and effort, the mean and variance in growth increment per molt, and natural mortality. Catch-length frequency and total fishing effort are available for most crab populations in Alaska. In this study we defined fishing effort as total annual pot lifts, i.e., the product of the total number of pots fished and the number of times each pot was deployed and retrieved in the fishery. The mean and variation in growth increment per molt can be estimated from tagging data, which are available for some crab populations.

In our study, we estimated the mean and variation in growth increments per molt for Bristol Bay and Kodiak RKC from studies by Balsiger (1974), Powell (1967), and Weber and Miyahara (1962). The model was fitted to RKC fishery data for Bristol Bay from 1974 to 1993 and for Kodiak from 1964 to 1982. Owing to low abundance, the Bristol Bay fishery was closed in 1994, and the Kodiak fishery has been closed since 1983. The RKC fisheries in Alaska harvest only male crabs, and the minimum legal carapace length (CL) is 135 mm for Bristol Bay RKC and 147 mm for Kodiak. Accordingly, we modeled only legal male crabs. The length frequency of catches was summarized by 5-mm intervals, and the largest length group included crabs ≥165 mm CL for Bristol Bay and ≥182 mm CL for Kodiak.

For comparisons, area-swept estimates of Bristol Bay legal male abundance were obtained from trawl surveys conducted by the National Marine Fisheries Service (NMFS) (Stevens et al.[1]). Standardized catch per unit of effort (CPUE) from pot surveys and from tag and recovery data for Kodiak legal male crabs was provided by Peterson et al. (1986). We estimated mean catchability of the Kodiak pot survey using the Petersen mark-recapture equation and annual commercial catch, tag, and recovery data from 1973 to 1979. This allowed us to estimate annual legal male abundances by dividing relative abundance (standardized survey CPUE) by the catchability. These abundance estimates derived from survey data were not used in catch-length analyses but were instead compared to final results of catch-length analyses.

Population model

The population model is similar to the length-based model for Bristol Bay RKC developed by Zheng et al. (1995). Mean growth increment per molt for length class i, G_i, is assumed to be a linear function of mean carapace length ι of the length class just before molting:

$$G_i = a + b\iota, \tag{1}$$

where a and b are the intercept and slope. Parameters a and b were estimated from Weber and Miyahara (1962) to be 13.140 and 0.018 for Bristol Bay, whereas we estimated them from Powell's (1967) data as 41.047 and –0.159 for waters off Kodiak Island.

For flexibility, we chose a gamma distribution to describe the variation in growth increment per molt:

$$g(x \mid \alpha_i, \beta) = x^{\alpha_i - 1} e^{-x/\beta} / \left(\beta^{\alpha_i} \Gamma(\alpha_i)\right), \tag{2}$$

where x is growth increment per molt, α_i and β are parameters, and $\alpha_i = G_i / \beta$. The expected proportion of crabs molting from length class i' to length class i is equal to the integral of the gamma function over the length interval $[i_1, i_2)$ of the receiving length class i:

$$P_{i',i} = \int_{i_1 - \iota}^{i_2 - \iota} g(x \mid \alpha_i, \beta)\, dx, \tag{3}$$

where ι is the mean length of length class i'. For the last length class L, $P_{L,L} = 1$. The variation in growth increment per molt, β, for both populations was set to 0.75, which produced a transitional matrix similar to that estimated by Balsiger (1974) for Bristol Bay RKC.

[1] Stevens, B. G., R. A. MacIntosh, J. A. Haaga, and J. H. Bowerman. 1993. Report to industry on the 1993 eastern Bering Sea crab survey. Alaska Fish. Sci. Center., Natl. Mar. Fish. Serv., NOAA, Seattle, WA, Proc. Rep. 93-14, 53 p.

The molting probability for a given length class and time t is modeled by a logistic function:

$$m_{i,t} = 1 - \frac{1}{1+\phi_t e^{-\omega_t \iota}}, \quad (4)$$

where ϕ_t and ω_t are parameters, and ι is the mean length of length class i. Different logistic functions were used to describe the molting probabilities during different periods. The molting probabilities during different years were grouped to produce a good fit. Three groups were selected for the Bristol Bay RKC: group 1 includes 1974–76, 1980, 1987–88, and 1992–93; group 2 covers 1981–86; and group 3 includes 1977–79 and 1989–91. Two groups were made for the Kodiak RKC: group 1 includes 1964–65, 1972, and 1980–82 and group 2 includes 1966–71 and 1973–79.

Recruitment into the exploitable population is separated into two components: 1) total recruits for year t entering the exploitable population, R_t, and 2) the proportion of recruits belonging to each length class, U_i. This is expressed by

$$R_{i,t} = R_t U_i, \quad (5)$$

where U_i is described by a gamma distribution for flexibility, such as in Equations 2 and 3, with parameters α_r and β_r.

To reduce the number of parameters, we assumed that new-shell and old-shell crabs have the same natural mortality and probability of molting the following year (Zheng et al., 1995). The annual abundance of new-shell crabs is the combined result of growth, mortality, and recruitment:

$$N_{i+1,t+1} = \sum_{i'=1}^{i+1}\left[P_{i',i+1}\left(\left(N_{i',t}+O_{i',t}\right)e^{-M} - \sum_p\left[\left(CN_{i',t,p}+CO_{i',t,p}\right)e^{(T_{t,p}-1)M}\right]\right)m_{i',t}\right] \times + R_{i+1,t+1}, \quad (6)$$

where $N_{i,t}$ and $O_{i,t}$ are the respective abundances of new-shell and old-shell crabs in length class i on 1 July in year t; $CN_{i,t,p}$ and $CO_{i,t,p}$ are the commercial catches of new-shell and old-shell crabs in length class i, year t, and fishing period p; M is instantaneous natural mortality; and $T_{t,p}$ is the period from 1 July to the mid-point of fishing period p in year t. All recruits are new-shell crabs. Old-shell crabs are crabs that did not molt the previous year:

$$O_{i+1,t+1} = \left(\left(N_{i+1,t}+O_{i+1,t}\right)e^{-M} - \sum_p\left[\left(CN_{i+1,t,p}+CO_{i+1,t,p}\right)e^{(T_{t,p}-1)M}\right]\right)(1-m_{i+1,t}). \quad (7)$$

The new-shell and old-shell crabs in the last length class were lumped together.

There was only one fishing period each year for the Bristol Bay RKC fishery and for the Kodiak RKC fishery prior to 1974. A second fishing period that targeted large crabs occurred for the Kodiak fishery each year from 1974 to 1982. The catch in the second fishing period was about 10% of that in the first period. We did not use the fishing efforts in the second period because the efforts targeted only a small proportion of the population and were relatively small.

For the first fishing period, the catch by length was estimated as

$$CN_{i,t,1} = TC_{t,1}s_{i,1}N_{i,t}/TB_{t,1},$$
$$CO_{i,t,1} = TC_{t,1}s_{i,1}O_{i,t}/TB_{t,1}, \quad (8)$$

where $TC_{t,1}$ is total annual observed catch for the first fishing period, and $TB_{t,1}$ is estimated exploitable abundance on 1 July in year t, i.e.

$$TB_{t,1} = \sum_i\left[s_{i,1}\left(N_{i,t}+O_{i,t}\right)\right], \quad (9)$$

and $s_{i,1}$ is the selectivity coefficient in length class i for the first fishing period. Parameters $s_{1,1}$ and $s_{2,1}$ were estimated for each population, and selectivity coefficients for length class 3 or larger were set to one.

The annual fishing effort for the first fishing period was

$$f_t = TC_{t,1}/(qMB_{t,1}), \quad (10)$$

where q is catchability coefficient for the fishery and $MB_{t,1}$ is mean exploitable abundance during the first fishing period in year t and approximated as

$$MB_{t,1} = TB_{t,1}e^{-T_{t,1}M} - 0.5TC_{t,1}. \quad (11)$$

During the second fishing period for the Kodiak RKC fishery, there were minimum size limits of 168 mm CL from 1974 to 1977, and 157.5 mm CL from 1978 to 1982. Two parameter values, θ_{s1} and θ_{s2}, were estimated for the two minimum size limits:

$$s_{i,t,2} = (e^{(\iota-\iota')^2\theta_{st}} - 1)/s_{L,t,2}, \quad (12)$$

where ι is the mean length of length class i, and ι' and L are the mean lengths of the first and last length classes. This selectivity function was chosen, based on the differences of the catch-length frequencies between the first and second fishing periods.

The catch by length for the second fishing period was estimated as

$$CN_{i,t,2} = TC_{t,2}\, s_{i,t,2}(N_{i,t}\, e^{-T_{t,1}M} - CN_{i,t,1})/TB_{t,2},$$
$$CO_{i,t,2} = TC_{t,2}\, s_{i,t,2}(O_{i,t}\, e^{-T_{t,1}M} - CO_{i,t,1})/TB_{t,2}, \quad (13)$$

where $TC_{t,2}$ is total annual observed catch for the second fishing period and $TB_{t,2}$ is estimated exploitable abundance just after the first fishing period in year t, i.e.

$$TB_{t,2} = \sum_i \left[s_{i,t,2} \begin{pmatrix} (N_{i,t} + O_{i,t}) e^{-T_{t,1}M} \\ - CN_{i,t,1} - CO_{i,t,1} \end{pmatrix} \right]. \quad (14)$$

Parameter estimation

Model parameters were estimated under the assumption of log normally distributed measurement or observation errors for length compositions of catches and annual fishing efforts. In Alaska, catch data are legally required for sales transactions between fishermen and processors, and it is generally believed that total annual crab catches in Alaska are fairly accurately reported. Thus, no measurement error was imposed on total annual catch for the catch-length analysis. A nonlinear least squares approach was used to minimize the residual sum of squares (RSS) of length compositions of catches and annual effort:

$$RSS = \sum_{i,t,p} \left[\begin{pmatrix} \left(\ln(CN_{i,t,p} + c) - \ln(\tilde{CN}_{i,t,p} + c)\right)^2 + \\ \left(\ln(CO_{i,t,p} + c) - \ln(\tilde{CO}_{i,t,p} + c)\right)^2 \end{pmatrix} \right] \quad (15)$$
$$+ \lambda^2 \sum_t \left[\left(\ln(f_t + 1) - \ln(\tilde{f}_t + 1)\right)^2 \right],$$

where $\tilde{CN}_{i,t,p}$ and $\tilde{CO}_{i,t,p}$ are observed catches for new-shell and old-shell crabs in length class i, year t, and fishing period p; f_t is observed fishing effort in year t for the first fishing period each year; λ is an error weighting factor for fishing effort relative to catch composition; and c is a constant set equal to 0.01×10^6 crabs to avoid taking the logarithm of zero and to reduce the impact of extremely small catches on parameter estimation. Generally, c should be relatively small compared to total catch, but estimation may fail to converge for a very small c.

The subroutine DBCLSF of IMSL FORTRAN (IMSL, 1991) was used to perform nonlinear least-squares parameter estimation through a modified Levenberg-Marquardt algorithm and a finite-difference Jacobian. All parameters were bounded to be nonnegative.

The following model parameters were estimated for each population: recruits for each year, except the first year; total abundance in the first year; parameters α_r and β_r; molting probability parameters ϕ_t and ω_t; selectivity parameters $s_{1,1}$, $s_{2,1}$, θ_{s1} and θ_{s2}; and catchability coefficient q. Starting in the second year, the abundances by length, sex, and shell condition were computed recursively from 1) the abundances by length and shell condition in the first year, 2) annual recruitment, 3) catch, and 4) model parameters. To reduce parameters further, we used the observed frequencies of length and shell classes from first-year catch data to approximate the true catch frequencies. Thus, we had to estimate only total abundance of male crabs for the first year.

Initial values of parameters were approximated by using catch data. A 40% harvest rate was used to convert total catch in the first year into total abundance and the sum of the new-shell catch in the first four length classes each year into recruitment (Zheng et al., 1995). Initial values were interactively updated; the estimated parameters for the first run were used as the initial parameters for the second run, and so on, until no further reduction of total RSS could be made.

Because we did not know the ratio between the variance of catch by length and the variance of fishing effort, we could not use a maximum likelihood approach. Instead, we used seven error weighting factors (λ): 0, 1, 2, 3, 5, 7, and 10 to conduct alternative catch-length analyses and compared the results for different weighting factors.

We did not estimate natural mortality but used several natural mortalities for comparisons. Kruse and Collie[2] and Collie[3] used 0.3 as instantaneous natural mortality for the Bristol Bay and Kodiak le-

[2] Kruse, G. H., and J. S. Collie. 1991. Preliminary application of a population size estimation model to the Bristol Bay stock of red king crabs. Alaska Dep. Fish Game, Comm. Fish. Div., Reg. Information Rep. 5J91-09, 25 p.

[3] Collie, J. S. 1991. Estimating the abundance of king crab populations from commercial catch and research survey data. Rep. to Alaska Dep. Fish Game. Univ. Alaska, Fairbanks, Rep. 91-03, 27 p.

gal male RKC. Besides 0.3, we also used M of 0.2, 0.4, and 0.5 in our analyses for both populations. In addition, variable natural mortalities—0.2 for periods of 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82—were used for the Bristol Bay population for comparisons based on our previous work with this stock (Zheng et al., 1995).

Results

Bristol Bay red king crab

Model parameter estimates for Bristol Bay RKC depend on natural mortality and weighting factor (Table 1). Higher natural mortality generally resulted in a higher total abundance in the first year and higher annual recruitment. Higher weights applied to fishing effort produced larger total *RSS*, whereas an intermediate weight resulted in the highest *RSS* contributed by the fishing effort (Table 1). For a weighting factor of one, total *RSS* were similar and ranged from 23.4 to 24.8 for all fits (Table 1). Catchability coefficient was negatively associated with natural mortality. Selectivity coefficients were less than one for the first length class for all fits and equal to about one for all other length classes.

The abundances of Bristol Bay legal male RKC estimated from the trawl surveys conducted by NMFS changed dramatically during the last two

Table 1

Summary of parameter estimates by the catch-length analysis for the Bristol Bay red king crab, *Paralithodes camtschaticus*, population for eight fits. Recruits are in thousands of crabs. Variable M is 0.2 for 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82. Total *RSS* (RSS_{tot}) is equal to the *RSS* of length compositions of catches (RSS_c) and annual effort (RSS_e).

	M=0.3 λ=0	M=0.3 λ=1	M=0.3 λ=3	M=0.3 λ=10	M=0.2 λ=1	M=0.4 λ=1	M=0.5 λ=1	M=var λ=1
α_r	232.743	244.608	194.611	188.020	222.013	208.456	182.513	223.248
β_r	0.6127	0.5824	0.7249	0.7546	0.6407	0.6761	0.7664	0.6355
ϕ_1	138,820	76,821	105,956	20,075	99,974	257,671	388,794	182,935
ω_1	0.0805	0.0750	0.0763	0.0658	0.0770	0.0832	0.0864	0.0812
ϕ_2	5,193.0	5,136.2	5,157.8	2,699.4	5,424.3	2,818.5	1,797.6	4,666.4
ω_2	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000	0.2000
ϕ_3	385,353	4,634,955	3,093,737	579,222	1,537,110	10,721,570	5,192,095	2,621,660
ω_3	0.0773	0.0944	0.0935	0.0836	0.0876	0.1001	0.0954	0.0906
q	NA	0.0023	0.0022	0.0024	0.0028	0.0019	0.0016	0.0024
$S_{1,1}$	0.9834	0.9008	0.8289	0.9379	0.9520	0.7820	0.7412	0.8329
$S_{2,1}$	0.9974	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
N_{74}	19,732.5	21,360.0	20,537.7	18,295.4	17,630.4	25,811.1	31,131.7	18,345.1
R_{75}	15,852.5	16,650.6	16,700.4	16,446.1	14,052.6	19,849.8	23,623.7	14,647.9
R_{76}	14,501.8	14,250.6	13,648.1	13,131.0	12,358.8	16,829.6	19,824.2	12,922.0
R_{77}	24,927.0	22,896.5	17,450.5	13,745.3	18,518.2	27,286.2	32,225.9	21,283.3
R_{78}	34,971.4	34,473.4	27,690.5	22,081.5	26,614.2	40,847.3	47,167.4	33,598.9
R_{79}	24,073.3	25,932.3	27,849.9	28,343.4	23,378.7	29,761.8	33,153.0	27,839.3
R_{80}	18,409.0	19,090.3	22,253.7	21,837.6	19,488.9	20,820.4	22,445.6	25,626.7
R_{81}	1,958.6	2,096.8	2,299.2	3,230.2	1,995.5	2,243.9	2,437.9	3,178.3
R_{82}	354.1	997.2	1,452.6	1,111.6	787.7	1,404.6	1,986.8	1,502.9
R_{83}	547.6	149.8	286.6	229.0	135.9	157.0	174.2	774.0
R_{84}	1,084.5	1,333.0	2,111.7	2,411.7	1,094.2	1,694.5	2,240.7	1,559.8
R_{85}	1,343.6	1,602.3	2.208.4	2,350.4	1,292.2	2,059.8	2,749.6	1,345.3
R_{86}	2,582.5	2,830.2	3,071.4	3,297.8	2,318.2	3,559.0	4,622.2	2,405.0
R_{87}	4,437.1	5,201.8	4,268.0	2,782.2	3,815.0	6,867.2	9,075.5	4,066.3
R_{88}	5,317.7	5,223.7	3,535.5	2,759.2	3,793.1	6,895.0	9,125.6	4,131.9
R_{89}	7,244.1	6,304.6	4,104.7	3,043.8	4,785.9	8,000.4	10,285.6	5,269.1
R_{90}	4,616.4	4,792.3	5,413.8	5,681.4	4,034.9	5,866.9	7,268.1	4,194.0
R_{91}	4,134.6	4,396.6	5,020.9	4,858.1	3,704.9	5,424.8	6,758.2	3,894.6
R_{92}	1,420.0	1,527.6	1,713.1	1,357.2	1,293.8	1,879.8	2,322.0	1,382.3
R_{93}	3,489.0	3,489.4	4,126.9	4,234.4	2,953.3	4,182.8	5,090.3	3,393.6
RSS_{tot}	19.957	24.659	35.028	45.685	24.844	23.999	23.782	23.356
RSS_c	19.957	20.999	30.030	42.629	21.437	20.595	20.461	19.839
RSS_e	0.000	3.660	4.998	3.056	3.407	3.404	3.321	3.517

decades (Stevens et al.[1]). The abundances peaked in the late 1970's and then declined more than 30-fold during the early 1980's (Fig. 1). A moderate recovery occurred in the late 1980's and early 1990's; then abundances decreased again during the last three years. The estimated abundances by different weighting factors with natural mortality of 0.3 generally reflected this trend of crab abundance with different accuracies, although modeled estimates were generally lower than the survey abundances (Fig. 1). The commercial CPUE was adjusted to the same scale as abundances to facilitate comparison, but it did not track well with the abundance trend estimated from the trawl surveys. The CPUE's were much higher in 1974 and 1975 and much lower in 1977 and 1978 than expected from the survey data. The CPUE's from 1984 to 1993 fluctuated around a low level, whereas the abundance increased and then decreased during the same period (Fig. 1). The estimated abundances from catch-length analyses with $\lambda = 0$ and $\lambda = 1$ were very similar, but the abundances in recent years tended to increase beyond a reasonable level without constraints on fishing effort or the recruitment in the terminal year for $\lambda = 0$. The upper limit of recruitment in the terminal year (1993) with $\lambda = 0$ was set to that estimated with $\lambda = 1$ to stabilize estimates. High weighting factor, $\lambda = 3$ or $\lambda = 10$, forced the abundance estimates close to the trend of CPUE. Overall the estimated abundance with $\lambda = 1$ most closely followed the trend of survey abundances (Fig. 1).

The estimated abundances with different instantaneous natural mortality rates followed the trend of survey abundances, and higher natural mortalities resulted in higher abundance estimates (Fig. 2). Generally, $M = 0.4$ produced absolute abundance estimates closer to the trawl survey than other natural mortalities. Variable natural mortality, expressed as three different levels, produced abundance estimates between those with M of 0.2 and 0.5, providing improvement in abundance estimates only during the early 1980's when high natural mortality occurred (Fig. 2).

The observed catches by length were compared to estimated catches by length from the model fit with $\lambda = 1$, with constant M of 0.3 and 0.5, and with three levels of M (Fig. 3). All three fits of the model produced similar catches by length and fit the observed data very well.

The observed and estimated fishing efforts have a similar overall trend but differed by up to 50% in some years (Fig. 4). As expected, larger weighting factors resulted in estimates of fishing effort closer to the observed level.

To explore further the effects of parameters λ and M on model results, we compared estimated length compositions of recruits and molting probabilities for the two most disparate fits (Fig. 5). There was very little variation in length compositions of recruits among different fits. The difference in molting probabilities was less than 15% between any two fits for any given length class within the same time period (Fig. 5) and was less than 5% among most fits for a given length class. The average molting probabilities from all fits for the first group of years were similar to the average molting probabilities estimated by Zheng et al. (1995) from the survey data with one exception. The molting probabilities for the period 1980–

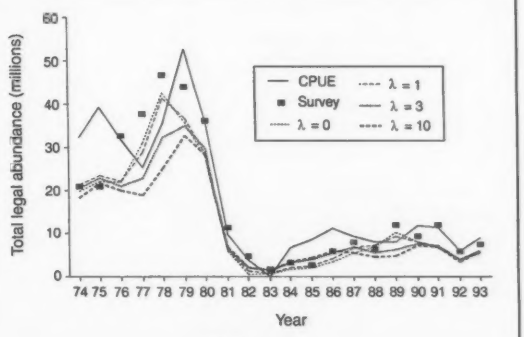

Figure 1

Comparison of estimates of total legal male abundance for Bristol Bay red king crab, with $M = 0.3$ and with different weighting factors (λ). The fishery CPUE (mean catch of legal male crabs per pot lift) was scaled to the same level as abundances. Also shown are NMFS trawl survey estimates of abundance.

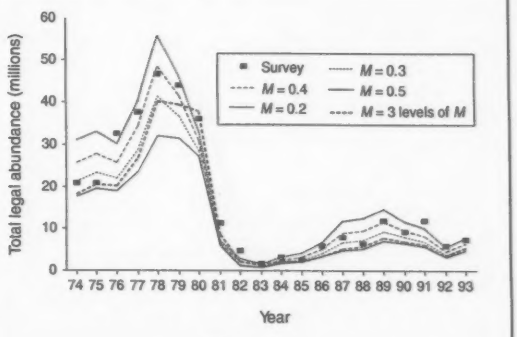

Figure 2

Comparison of estimates of total legal male abundance for Bristol Bay red king crab modeled with weighting factor $\lambda = 1$ and with either constant or variable M at three levels: 0.2 for 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82. Trawl survey estimates of abundance are also shown for comparison.

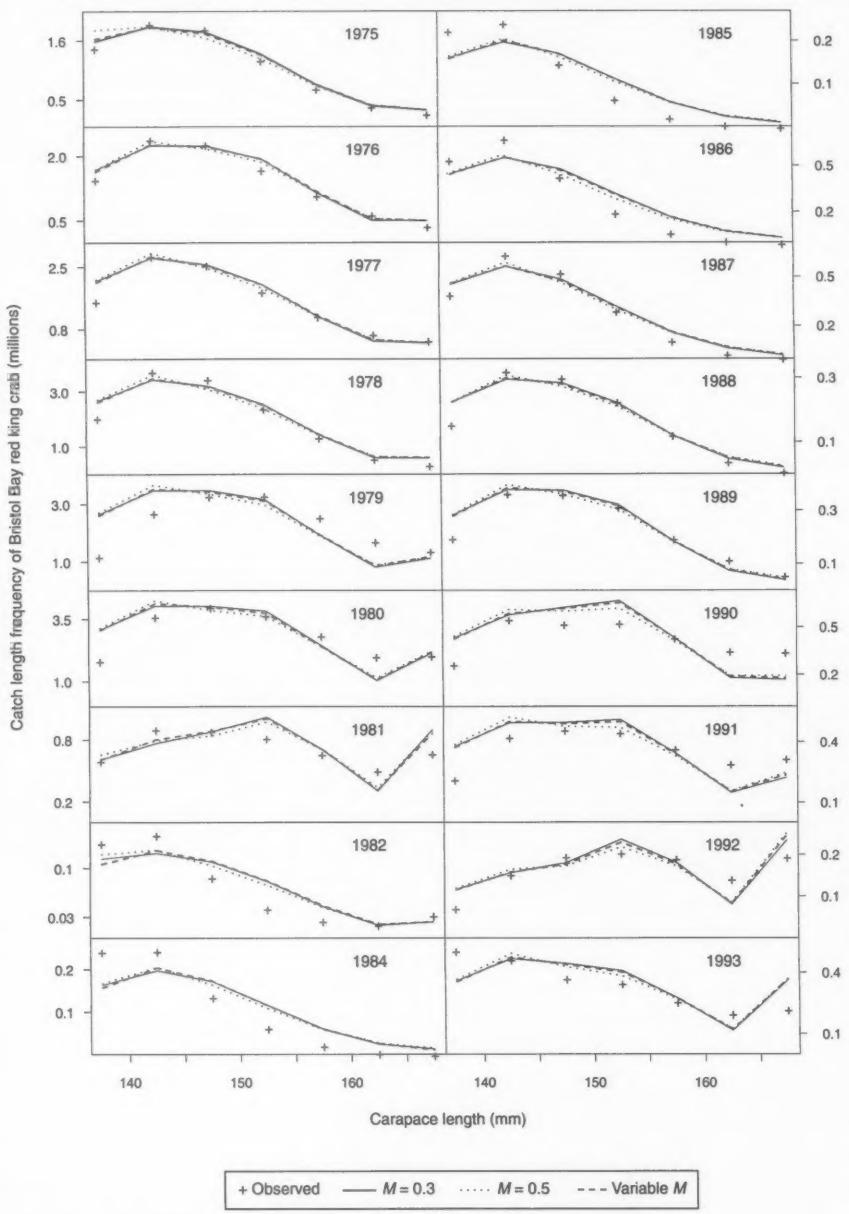

Figure 3

Comparison of observed and estimated length frequencies of Bristol Bay red king crab catches modeled with weighting factor $\lambda = 1$, constant M of 0.3 and 0.5, and with three levels of M (0.2 for 1974–79 and 1985–93, 0.7 for 1980 and 1983–84, and 1.2 for 1981–82).

86 were estimated to be zero, which is biologically unrealistic. The zero molting probabilities were primarily caused by few large new-shell crabs in the catch during this period. The average molting probabilities from all fits during 1977–79 and 1989–91 were slightly higher than those estimated by Zheng et al. (1995).

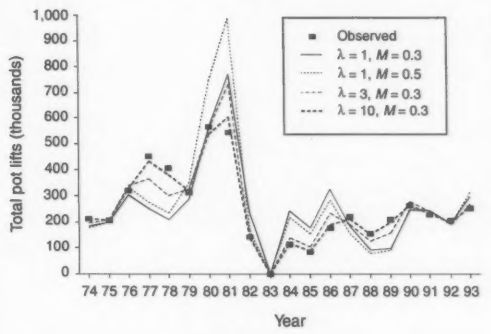

Figure 4

Comparison of observed and estimated fishing efforts of the Bristol Bay red king crab fishery modeled with weighting factor $\lambda = 1$ and constant M of 0.3 and 0.5 and with weighting factor $\lambda = 3$ and 10 and constant M of 0.3.

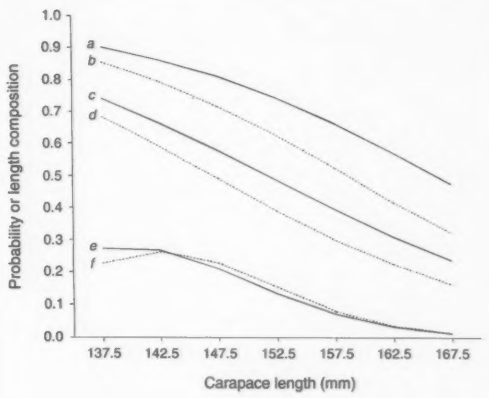

Figure 5

Comparisons of length compositions of recruits (e: λ=0 and M=0.3, f: λ=10 and M=0.3), molting probabilities during periods 1974–76, 1980, 1987–88, and 1992–93 (c: λ=5 and M=0.3, d: λ=1 and M=0.3), and during periods 1977–79 and 1989–91 (a: λ=1 and M=0.5, b: λ=0 and M=0.3) from the two most disparate fits among all model fits for Bristol Bay red king crab.

Kodiak Island red king crab

As in the case of Bristol Bay RKC, the abundance in the first year and annual recruitment of red king crab off Kodiak Island were mainly affected by natural mortality and the weighting factor (Table 2). For all fits, the recruitment in 1965 was much higher than those in other years. With $\lambda = 1$, total *RSS* decreased slightly with increasing natural mortality, whereas the *RSS* contributed by fishing effort increased (Table 2). Higher weighting factors resulted in higher total *RSS* (Table 2). For the first fishing period, selectivity coefficients for the first length class were about 0.5, and no selectivity was detected for the other length classes (Table 2). For the second fishing period, catches concentrated on large-size crabs.

The estimated legal male abundances of Kodiak RKC peaked in 1965 and fell to a very low level in the late 1960's (Fig. 6). The population moderately recovered in the early and middle 1970's but declined again in the late 1970's and completely collapsed after 1982. Model estimates of abundance with M = 0.3 and different weighting factors basically followed the same trends as the fishery CPUE and the abundances estimated by pot surveys (Fig. 6). Note that no survey data were available until 1973 (Peterson et al., 1986). Like the results for Bristol Bay RKC, the abundance estimates with $\lambda = 1$ followed the trend of survey abundances best among all fits. The scaled CPUE was very close to survey abundance estimates from 1973 to 1977 but were much lower from 1978 to 1981.

Similar to Bristol Bay RKC, the estimated abundances for Kodiak RKC with different natural mortalities had a similar trend over time, and a higher natural mortality produced higher abundance estimates (Fig. 7). The estimated abundances with natural mortality of 0.2 were lower than survey abundances for most years, whereas the abundances estimated with natural mortality of 0.5 were generally higher. With M = 0.4, the closest abundance estimates to survey abundances were produced among all fits (Fig. 7).

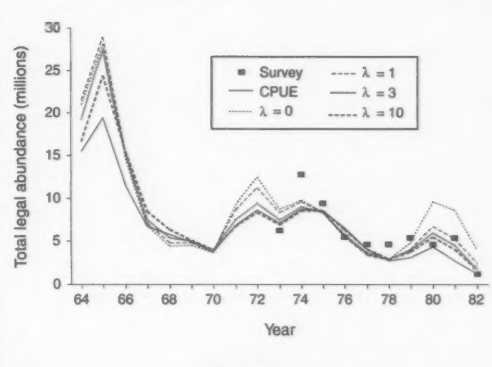

Figure 6

Comparison of estimates of total legal male abundance for Kodiak red king crab with M of 0.3 and different weighting factors (λ). The fishery CPUE was scaled to the same level as abundances.

Table 2

Summary of parameter estimates by the catch-length analysis for the Kodiak red king crab population for seven fits. Recruits are in thousands of crabs. Total *RSS* (RSS_{tot}) is equal to the *RSS* of length compositions of catches (RSS_c) and annual effort (RSS_e).

	M=0.3 λ=0	M=0.3 λ=1	M=0.3 λ=3	M=0.3 λ=10	M=0.2 λ=1	M=0.4 λ=1	M=0.5 λ=1
α_r	81.727	35.562	39.570	34.371	39.576	33.364	37.299
β_r	1.7562	3.4703	3.2294	3.6075	3.2052	3.6289	3.2795
ϕ_1	147,272	135,590	134,336	246,181	121,736	142,585	656,736
ω_1	0.0674	0.0679	0.0684	0.0732	0.0671	0.0683	0.0769
ϕ_2	258,686	5,900,997	5,859,429	6,001,626	5,215,578	5,681,410	3,532,557
ω_2	0.0787	0.0982	0.0981	0.0981	0.0972	0.0982	0.0952
q	NA	0.0045	0.0047	0.0048	0.0050	0.0038	0.0029
$S_{1,1}$	0.5520	0.4481	0.4649	0.4560	0.4538	0.4466	0.4460
$S_{2,1}$	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000
θ_{s1}	1.0e-6	1.0e-6	1.0e-6	0.0003	1.0e-6	0.0002	0.0004
θ_{s2}	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6	1.0e-6
N_{64}	20,944.8	21,537.4	19,273.2	16,664.7	18,173.0	25,863.5	32,485.1
R_{65}	17,684.0	18,482.6	18,412.5	17,298.9	16,460.5	20,938.2	24,625.0
R_{66}	4,592.4	5,330.7	6,662.2	8,951.2	4,873.5	5,831.0	6,222.7
R_{67}	2,796.0	3,078.2	3,647.5	5,127.5	2,798.5	3,417.3	3,878.6
R_{68}	3,316.6	3,619.0	4,046.4	4,529.1	3,164.2	4,274.9	5,632.4
R_{69}	3,461.8	3,621.5	3,525.1	3,125.5	3,045.6	4,492.4	6,385.9
R_{70}	2,121.7	2,158.9	2,043.8	2,029.3	1,795.0	2,707.4	3,880.0
R_{71}	8,046.7	7,480.9	6,209.6	5,328.2	5,918.3	9,819.2	15,043.5
R_{72}	8,586.0	7,634.8	6,320.9	5,610.1	6,186.2	9,740.1	14,467.9
R_{73}	4,095.6	4,263.0	4,037.3	3,766.8	3,574.5	5,190.1	6,710.2
R_{74}	5,185.5	5,405.2	5,448.1	5,466.6	4,647.3	6,423.0	8,182.8
R_{75}	4,116.1	4,407.9	4,809.2	5,360.7	3,835.2	5,143.3	6,362.9
R_{76}	2,266.6	2,464.4	2,753.0	3,264.4	2,152.7	2,859.6	3,463.3
R_{77}	1,416.1	1,495.0	1,599.8	1,835.6	1,323.9	1,702.9	2,033.7
R_{78}	1,837.0	1,816.9	1,723.0	1,573.6	1,645.5	2,034.8	2,493.3
R_{79}	4,074.1	3,510.5	3,232.3	3,008.8	3,210.3	3,956.7	5,256.6
R_{80}	8,327.1	5,879.3	5,147.0	4,672.7	5,410.7	6,762.5	9,835.9
R_{81}	6,295.2	4,101.1	3,556.5	3,271.2	3,825.8	4,814.7	6,714.1
R_{82}	1,889.0	1,888.9	1,400.1	1,474.6	1,773.6	2,230.5	2,315.5
RSS_{tot}	35.584	41.165	46.751	53.170	42.361	39.801	36.519
RSS_c	35.584	39.828	43.379	51.876	40.908	38.176	34.181
RSS_e	0.000	1.337	3.372	1.294	1.453	1.625	2.338

The observed catches by length were compared to estimated catches by length from the model fit with $\lambda = 1$ and with constant M of 0.3, 0.4, and 0.5 (Fig. 8). All three fits of the model produced similar catches by length and fitted the observed data very well, except data for 1965 and 1982. The poor fit in 1965 was mainly caused by the observed catch-length composition in the initial year (1964). The rapid expansion of fishing grounds during this period made the catch-length compositions inconsistent between these two years. The catch in 1982 was extremely low in comparison to the past annual catches.

The fishing effort was very high during the mid-1960's and the early 1980's (Fig. 9). Like Bristol Bay RKC, larger weighting factors produced estimates of fishing effort closer to the observed effort. With $\lambda = 1$, a constant M of 0.3 fitted the fishing effort much better than a constant M of 0.5 (Fig. 9).

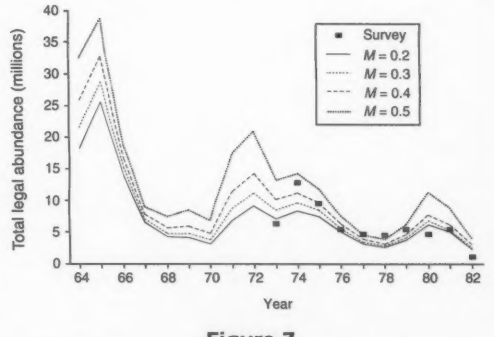

Figure 7

Comparison of estimates of total legal male abundance for Kodiak red king crab modeled with weighting factor $\lambda = 1$ and different values of M.

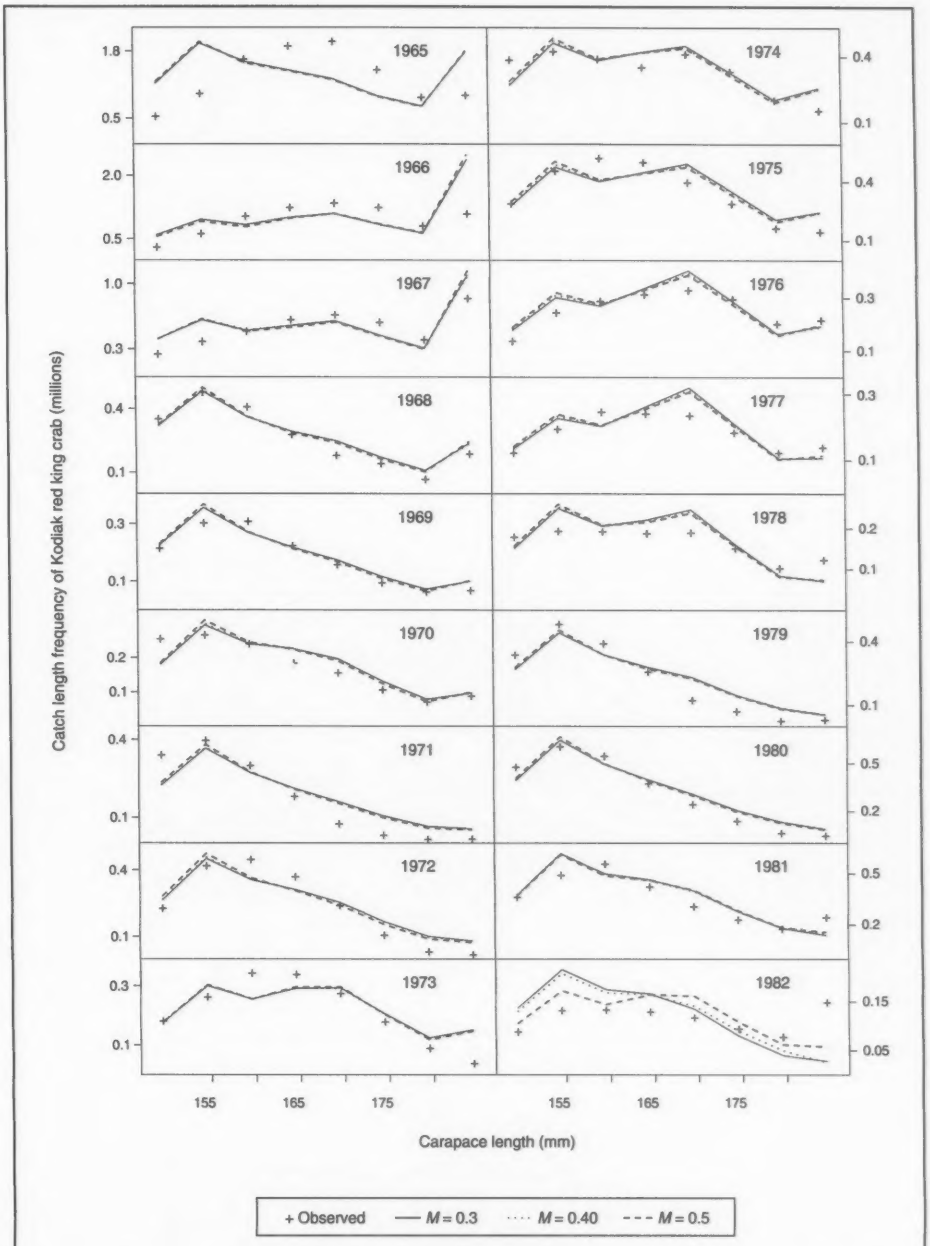

Figure 8

Comparison of observed and estimated length frequencies of Kodiak red king crab catches modeled with weighting factor $\lambda = 1$ and with a constant M of 0.3, 0.4, and 0.5.

Similar to Bristol Bay RKC, there was very little difference in length compositions of recruits among all fits (Fig. 10). The difference in molting probabilities was generally less than 10% between any two fits for any given length class (Fig. 10) and was less than 2% among most fits for a given length class. Molting probabilities for the first group of years were much higher than the second group.

Discussion

Two alternative models have been developed for RKC populations. A measurement error model using catch and survey data was developed to smooth out measurement errors in abundance estimates of legal male crabs composed of two groups: recruits and post-recruits (Collie and Kruse, in press; Kruse and Collie[2]; Collie[3]). The expanded version of the measurement error model is a length-based population model that incorporates stochastic growth and gradual recruitment over length and that estimates abundances of mature crabs of both sexes (Zheng et al., 1995). The length-based model also provides a means to study stock-recruitment relationships and can be used to evaluate harvest strategies. The catch-length analysis we developed in this study is a simplified version of the length-based model constructed by Zheng et al. (1995) and is meant to be applied to crab populations for which no surveys are conducted. The length-based model estimates abundance by producing the best fit to length-frequency data from the survey, and the catch-length analysis estimates abundance by producing the best fit to length-frequency and fishing-effort data from the commercial fleet. The catch-length analysis generally provides accurate estimates of trends of relative population abundances and gives reasonable estimates of absolute abundances provided that M can be approximated.

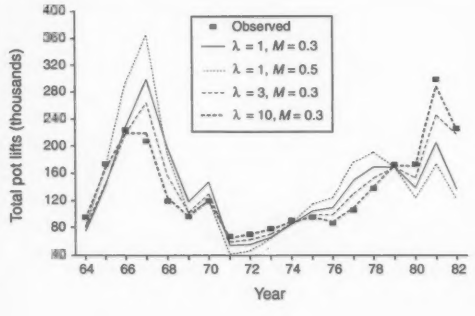

Figure 9

Comparison of observed and estimated fishing efforts of the Kodiak red king crab fishery modeled with weighting factor $\lambda = 1$ and constant M of 0.3 and 0.5 and with weighting factor $\lambda = 3$ and 10 and constant M of 0.3.

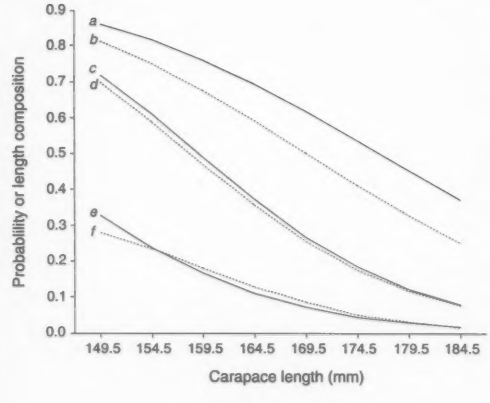

Figure 10

Comparisons of length compositions of recruits (e: λ=0 and M=0.3, f: λ=10 and M=0.3), molting probabilities during periods 1966–71 and 1973–79 (c: λ=1 and M=0.2, d: λ=1 and M=0.5), and during periods 1964–65, 1972, and 1980–82 (a: λ=1 and M=0.5, b: λ=0 and M=0.3) from the two most disparate fits among all model fits for Kodiak red king crab.

The legal male crab abundances estimated from the survey data for both populations were assumed to be absolute and were used to gauge the reliability of the catch-length analysis. A systematic approach was used to survey both populations with complete coverage of areas occupied by large-size crabs (Peterson et al., 1986; Stevens et al.[1]). The length frequency of crabs caught by the survey gears in Bristol Bay and Kodiak indicated that the selectivity of legal male crabs is about equal to one. Catchability of survey gears is difficult to estimate. Zheng et al. (1995) assumed the catchability of the trawl survey for Bristol Bay legal male RKC to be one, and Collie and Kruse (in press) showed that catchabilities of legal male RKC for both populations are close to one. Therefore, our assumption of absolute crab abundances from the survey estimates is reasonable. If this assumption is invalid, the survey abundances still represent relative population abundances, but we cannot use them to compare different levels of natural mortality in the catch-length analysis.

The most important parameter affecting total abundance estimates from the catch-length analysis is M, which has to be estimated separately from the analysis. Published natural mortalities for RKC vary greatly from one study to another and are probably a function of time and length (Schmidt and Pengilly, 1993; Zheng et al., 1995). A constant M of 0.3 was assumed for both Bristol Bay and Kodiak legal male RKC (Kruse and Collie[2]; Collie[3]; NPFMC[4]). Our re-

[4] NPFMC (North Pacific Fishery Management Council). 1990. Environmental assessment for Amendment 1 to the fishery management plan for the commercial king and Tanner crab fisheries in the Bering Sea/Aleutian Islands. North Pacific Fishery Management Council, Anchorage, AK, 27 p.

sults indicate that a constant M of 0.4 provides population abundance estimates closest to the abundances estimated by survey data for both RKC populations. Unlike the results from Zheng et al. (1995), variable M over time improved only slightly the abundance estimates from catch-length analysis. Because it is difficult to estimate M for crab populations, we suggest that a sensitivity study should be conducted to examine the effect of M on estimated abundances. Although M affects absolute abundance greatly, relative abundance is fairly robust to changes in M. Thus, if we are mainly interested in recruitment or population trends, such as those used in fishery oceanography, then uncertainty of M is not a big concern. On the other hand, if we wish to manage an unsurveyed crab stock with a fixed exploitation rate strategy, M must be known fairly accurately in order to avoid consistent over- or under-harvest.

In contrast to M, weighting factor λ primarily affects the estimated trend of a population. By weighting fishing efforts heavily, the population trend most closely resembles the fishery CPUE. The CPUE for crab pots depends not only on exploitable crab abundance, but also on many other factors, such as pot size, soak time, bait, tidal cycle, and vessel characteristics. Pot size is limited by regulations in Alaska and has not changed much over time. Soak time is probably the most important factor but generally is not collected for crab fisheries. Tidal information is available, but the relationship between tidal condition and CPUE may be too complex to be used for effort standardization. Vessel characteristics can be used to adjust for temporal changes in fleet composition, but Johnson (1991) found that vessel characteristics do not effect the relationship between crab density and CPUE for the Kodiak RKC fishery from 1969 to 1982. The CPUE defined as catch per pot lift, which is available for most crab fisheries in Alaska, could explain only partial variation in crab densities. Therefore, heavy weighting of fishing effort would distort the true trend of crab abundance, whereas without fishing effort information the abundances in recent years have tended to be over-estimated. An error-weighting factor of one generally gave a good fit for both RKC populations.

Red king crab tend to aggregate by forming pods much in the same way that some fishes form schools. When crab abundance decreases, the area of distribution shrinks, and crab density in the remaining area is still relatively high. The overall geographic distribution of Bristol Bay RKC has gradually shrunk since crab abundances peaked in the late 1970's. Such aggregate or schooling behavior may produce depensatory catchability (Clark, 1974). When population abundances are low, depensatory catchability can easily result in overestimates of population abundances and overfishing if a constant catchability is assumed. On the other hand, when population abundances are high, abundances may be underestimated because of gear saturation (Bannerot and Austin, 1983). We modified Equation 10 in a manner described by Bannerot and Austin (1983) to compare the results between constant and density-dependent catchabilities. Overall, both relative and absolute abundances estimated under a constant catchability assumption fitted closer to the survey abundances for both populations than those fitted under an assumption of density-dependent catchability. It is conceivable that our fishery CPUE data may not have sufficient information to estimate density-dependent catchability.

As with conventional catch-age or cohort analyses, without auxiliary information there is great uncertainty in estimating the abundance in the terminal year by catch-length analyses. The accuracy of estimated absolute abundance in the terminal year depends on how accurately we can estimate fishing mortality. However, by incorporating fishing effort data, even with large measurement errors, it has been possible to estimate relative abundance trends rather well in most recent years. In cases where fishing effort is not available, an upper limit should be set for recruitment in the terminal year to avoid biasing the trend of relative abundances upward in the most recent years.

The selectivity coefficient for the first length class was estimated to be less than one for all scenarios; thus legal crabs with sizes close to the size limit appear to have a lower catchability. Legal male crabs have been mature for at least one or two years and theoretically should fully recruit to the fishing gear. But the observed catch-length frequency shows that length compositions of the first length class were smaller than those of the second length class for both fisheries and for all years except 1993. This selectivity may be partially caused by throwing back some barely legal-size crabs that were incorrectly measured by fishermen. The catch-length analysis may sometimes fail to estimate selectivity because selectivity coefficients and recruitment parameters may be confounded. A low proportion of recruitment to the first length class of new-shell crabs can cancel the effect of selectivity. We suggest that the selectivity coefficient for the first length class be interactively set to different values less than one during estimation until RSS cannot be further minimized. In recent years, observers have been placed on crab catcher and floater processors in Bristol Bay, and length frequency of the catch has been measured before sorting. In the future, comparison of the time series of length-frequency data on presorted and retained catches could

be used to estimate selectivity, and then selectivity could be fixed in catch-length analyses.

The trend of legal male abundances for Kodiak RKC is similar to that for Bristol Bay RKC, except that the Kodiak stock peaked 13 years prior to Bristol Bay. The high estimated abundance for the Kodiak population in the early 1960's may partly reflect expansion of the fleet to new fishing grounds (Spalinger[5]), whereas the peak abundance for the Bristol Bay population in the late 1970's resulted from strong recruitment (Zheng et al., 1995). Both populations decreased dramatically from their peak abundances within a few years and then fluctuated at low levels over time. When these two populations are examined over the same time scale, the trends are quite different. The abundance for the Bristol Bay population increased greatly from the early to late 1970's, whereas the abundance for the Kodiak population gradually decreased during the same period. The abundances for both populations decreased from 1980 to 1982. Since 1982 the Bristol Bay population has recovered a little, whereas the Kodiak population has completely collapsed and has not been able to support a fishery (Spalinger[5]).

Acknowledgments

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Allozyme variability in two samples of swordfish, *Xiphias gladius* L., in the North Pacific Ocean

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The swordfish, *Xiphias gladius* L., is a cosmopolitan species found in all tropical and temperate oceans (Nakamura, 1983). It is an esteemed food fish and subject to a multinational fishery throughout its range of distribution (Sakagawa, 1989). In 1991 the Pacific catch was 29,245 metric tons (t) or about 44% of the total global catch of 67,142 t (FAO, 1993).

A variety of population structures have been proposed for Pacific swordfish. From one to four stocks have been proposed on the basis of fishery data from all of the Pacific Ocean (Bartoo and Coan, 1989; Skillman, 1989; and Sosa-Nishizaki and Shimizu, 1991). Grijalva-Chon et al. (1994) examined restriction-fragment-length polymorphisms (RFLP) of mitochondrial DNA (mtDNA), and their results supported the hypothesis of one stock in the North Pacific.

Allozyme analyses have been used extensively to study population structure in fishes, especially in fishery resources, because of their relative simplicity (Utter et al., 1974, 1987; Ihssen et al., 1981). Several studies of mtDNA have demonstrated increased resolution for detecting population substructure (Ferris and Berg, 1987), and the methods used in them have complemented each other because they involve different modes of inheritance: with protein electrophoresis, phenotypic data from nuclear loci and from alleles transmitted by sexual reproduction can be analyzed, whereas with the mtDNA method, fragments of haploid DNA that are (usually) maternally inherited and evolve rapidly can be analyzed (Allendorf et al., 1987). The nuclear allelic variants involve sexual exchange among individuals, and one can infer the population fitness or reproductive success through genetic variation (Nevo, 1978). In the case of a fishery resource, fishing mortality alters the frequency of adaptative traits (Nelson and Soulé, 1987).

The intent of this study was to examine the genetic variation at protein-coding loci in swordfish in a preliminary way to test whether swordfish in two localities in the North Pacific were genetically homogeneous.

Materials and methods

Samples of white muscle, liver, and heart from 44 individuals from the N–NE Hawaiian Islands and from 50 individuals from Mexico off Baja California were used to study the allozymic variation (see Grijalva-Chon et al. [1994] for sampling and storage details).

Samples of approximately 5 g of tissue were homogenized in equal volumes of a solution consisting of 0.1 M Tris-HCl pH 8, NAD+, NADP, and polyvinylpyrrolidone (100:0.1:0.1:1, v:w:w:w), with an electric homogenizer (Tissumizer Tekmar). In the case of liver, 0.5 mL of toluene was added. Homogenized samples were centrifuged at 20,000 ×g for 20 minutes at 4°C, and supernatants transferred into capped tubes and stored at –70°C.

The allozyme analysis comprised 15 enzyme systems that encoded 26 presumptive loci (Table 1). In general, the method described by Aebersold et al. (1987) was followed, with the exception that agar was not used in the staining procedure. The support media were 12% starch gels (Sigma S4501).

The criteria of Grant and Utter (1980) and Grant et al. (1984) were followed for zymogram interpretation. Locus nomenclature followed that of Shaklee et al. (1990), which designates the loci in ascending order beginning with number 1 for the most cathodal locus. Alleles for polymorphic loci were designated by using relative electrophoretic mobilities: the most common allele at each locus was designated to be 100.

Data were analyzed with BIOSYS-1 (Swofford and Selander, 1981). A locus was considered poly-

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Table 1

Protein systems and loci resolved in North Pacific swordfish. Buffers: A = Continuous Tris-citratre II, pH 8.0 (Selander et al., 1971); B = Tris-maleate, pH 7.4 (Selander et al., 1971); C = Tris-EDTA-borate, pH 8.0 (Shaw and Prasad, 1970); D = Tris-citrate, pH 8.0 (Tracey et al., 1975); E = Aminopropyl-morpholine, pH 6.1 (Clayton and Tretiak, 1972). Stains: 1 = Shaw and Prasad (1970); 2 = Schaal and Anderson (1974); 3 = Rosa-Velez (1986). E.C.= Enzyme Commission number.

Enzyme or protein	E.C.	Locus	Tissue	Buffer	Stain
Lactate dehydrogenase	1.1.1.27	*LDH-1**	Heart	A	1
		*LDH-2**	Heart		
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-1**	Heart	A	1
		*GPI-2**	Heart		
Malic enzyme	1.1.1.40	*MEP**	Heart	A	2
Phosphoglucomutase	5.4.2.2	*PGM**	Muscle	A	2
Aspartate aminotransferase	2.6.1.1	*AAT-1**	Liver	A	2
		*AAT-2**	Liver		
Glucose-6-phosphate dehydrogenase	1.1.1.49	*G6PDH**	Heart	B	2
Xanthine dehydrogenase	1.1.1.204	*XDH**	Liver	C	2
Glutamate dehydrogenase	1.4.1.3	*GDH**	Liver	C	2
Acid phosphatase	3.1.3.2	*ACP-1**	Liver	D	1
		*ACP-2**	Liver		
Octanol dehydrogenase	1.1.1.73	*ODH**	Liver	D	1
Sorbitol dehydrogenase	1.1.1.14	*SDH-1**	Liver	D	2
		*SDH-2**	Liver		
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH**	Liver	D	2
General protein	—	*PROT-1**	Heart	D	3
		*PROT-2**	Heart		
		*PROT-3**	Muscle		
		*PROT-4**	Muscle		
Esterase	3.1.1.-	*EST**	Liver	E	1
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH-1**	Heart	E	2
		*GAPDH-2**	Heart		
		*GAPDH-3**	Heart		
		*GAPDH-4**	Heart		

morphic if the frequency of the most common allele did not exceed 0.95. The mean heterozygosity over all loci was computed following Nei's (1978) unbiased formula. The Hardy-Weinberg equilibrium hypothesis was tested for all polymorphic loci by means of a chi-square (χ^2) test, by pooling genotypes when more than two alleles were observed. Lavene's correction for small sample size and Yates's correction for continuity were applied (Swofford and Selander, 1981). Exact significance probabilities were calculated only to check concordance with the χ^2 test.

Genetic distance (Nei, 1978) between localities was computed. Also, the inbreeding coefficient, F_{is}, and the standarized variance in allelic frequencies, F_{st}, were calculated to measure the amount of divergence among subpopulations (Wright, 1965). The null hypothesis F_{is}=0 was tested by means of χ^2=$F_{is}{}^2n$, with $k(k-1)^2$ degrees of freedom, where k denotes number of alleles (Li and Horvitz, 1953). The null hypothesis F_{st}=0 was tested by means of χ^2=$F_{st}{}^2n$, with $(s-1)(k-1)$ degrees of freedom, where s denotes the number of geographic localities and k the number of alleles (Workman and Niswander, 1970). The heterogeneity of allelic frequencies at polymorphic loci among geographic localities was tested with the log-likelihood ratio test (G-test) with Yates's correction for continuity (Zar, 1984). The number of migrants per generation was estimated by N_em = $(F_{st}{}^{-1}-1)/4$ (Hartl, 1988).

Results

Four out of twenty-six loci were polymorphic: *ODH**, *GPI-1**, *PROT-2**, and *PROT-3**. Table 2 summarizes the genetic variation fish from both localities. The average number of alleles per locus was 1.19 (Mexico), and 1.31 (Hawaii). The observed heterozygosity per locus ranged between 0.000 and 0.341 (Table 3), with a mean of 0.010 in Mexico, and 0.026 in Hawaii. The mean gene diversity for the pooled data was 0.020.

Isocitrate dehydrogenase (IDH) revealed variation in a preliminary survey. Richardson et al. (1986) showed, however, that this enzyme may mimic a genetic polymorphism where in fact it is exhibiting age-related modification. The tissues samples were held

for 1 to 1.5 years at –70°C before analysis. Because of this, IDH was eliminated from the analysis.

Only one locus was out of Hardy-Weinberg equilibrium: *GPI-1** showed heterozygote deficiency in the Mexican sample (Table 3). This result was reflected in the F_{is} value for that locus (Table 4). The genetic distance between populations was very low: it varied between 0.000 and 0.014, with a mean of 0.0007 over all loci.

Table 2

Genetic variation of North Pacific swordfish. Standard errors are in parentheses.

	Mexico	Hawaii
No. of individuals	50	44
No. of loci examined	26	26
No. of polymorphic loci	2	2
Percentage of polymorphic loci	7.69	7.69
No. of alleles per locus	1.19 (0.08)	1.31 (0.11)
Average heterozygosity		
Observed	0.010 (0.005)	0.026 (0.014)
Expected	0.013 (0.006)	0.027 (0.013)

Table 4

Genetic distance, *G*-test for allelic frequencies heterogeneity, and *F*-statistics at polymorphic loci of North Pacific swordfish. * = $0.01 < P \leq 0.05$; ** = $0.001 < P \leq 0.01$; and *** = $P \leq 0.001$. *D* = genetic distance; *G* = *G*-test.

	D	*G*	F_{is}	F_{st}
*ODH**	0.001	0.615	–0.054	0.026 (*)
*GPI-1**	0.000	1.837	0.338 (***)	0.008
*PROT-2**	0.002	1.489	–0.082	0.030 (*)
*PROT-3**	0.014	4.851 (*)	–0.183	0.066 (***)
Totals		8.792 (*)	–0.013	0.039 (**)

Table 3

Allelic frequencies, heterozygosity, and Hardy-Weinberg expectations of phenotypes at four polymorphic loci. Number of individuals are in brackets. Differences in sample sizes were due to inactivation of enzymes. ns= not significant; ** = $P \leq 0.01$.

					Heterozygosity		Phenotype frequencies			
Locus	Locality	Allelic frequencies			Observed	Expected	Phenotype	Observed	Expected	Chi-square
		*100	*114							
*ODH**	Mexico [39]	0.949	0.051		0.103	0.099	A	0	0.780	0.000 (ns)
							AB	4	3.844	
							B	35	35.078	
	Hawaii [42]	1.000	0.000		0.000	0.000	A	0		
							AB	0		
							B	42		
		*75	*100	*119						
*GPI-1**	Mexico [50]	0.070	0.930	0.000	0.060	0.132	B	45	43.212	9.296 (**)
							BC	3	6.576	
							C	2	0.212	
	Hawaii [41]	0.024	0.963	0.012	0.073	0.072	A	0	0.000	0.000 (ns)
							AB	1	0.975	
							AC	0	0.025	
							B	38	38.037	
							BC	2	1.951	
							C	0	0.012	
		*100	*175							
*PROT-2**	Mexico [50]	0.990	0.010		0.020	0.020	A	0	0	0.000 (ns)
							AB	1	1	
							B	49	49	
	Hawaii [42]	0.917	0.083		0.167	0.155	A	0	0.253	0.000 (ns)
							AB	7	0.494	
							B	35	35.253	
		*100	*175							
*PROT-3**	Mexico [50]	0.980	0.020		0.040	0.040	A	0	0.010	0.000 (ns)
							AB	2	1.980	
							B	48	48.010	
	Hawaii [41]	0.829	0.171		0.341	0.287	A	0	1.123	0.619 (ns)
							AB	14	11.753	
							B	27	28.123	

The analysis of heterogeneity of allelic frequencies showed relatively small but significant differences (Table 4), with the total G=8.79 (P<0.05). The weighted average of F_{is} was –0.013, not different from zero (P>0.05), and the weighted average of F_{st} was 0.039, different from zero (P<0.001). Considering the F_{st} value, the estimated number of migrants per generation was 6.2.

Discussion

North Pacific swordfish exhibit low heterozygosity. The heterozygosity in swordfish, 0.020, is low compared with the averages of 0.055 (Smith and Fujio, 1982) and 0.064 (Ward et al., 1994) reported for marine fishes. For bony fishes in general, Nevo (1978) and Winans (1980) reported 0.051 and 0.048, respectively. The Pacific blue marlin, *Makaira nigricans*, another billfish, showed a mean heterozygosity of 0.06 (Shaklee et al., 1983).

Both *PROT-2** and *PROT-3** were polymorphic in the Hawaiian population; however, the latter was responsible for the significant differences in allelic frequencies. Although *PROT-3** drove the final result in the analysis of allelic frequencies, *ODH** and *PROT-2** also contributed in a significant way to the amount of divergence as denoted by F_{st}.

The locus *IDH** showed a high number of heterozygous organisms in the Hawaiian samples during the preliminary analysis, but that result was doubtful considering the delicate nature of that enzyme (Richardson et al., 1986). Future studies should use tissues that are as fresh as possible.

The observed heterogeneity in allelic frequencies among the two samples was an unexpected result. Recently, Grijalva-Chon et al. (1994) reported no differences in genotypic frequencies in a restriction analysis of mtDNA of North Pacific swordfish and could not reject the null hypothesis of a single population. Chow (1994) carried out PCR-RFLP analysis on the control region of mtDNA and found no differences in the haplotype frequencies between western (Japan) and eastern (Baja California) Pacific specimens of swordfish.

A widespread opinion is that mtDNA analysis is a more sensitive approach for defining population structure than are allozymes (Ferris and Berg, 1987). In fact, many studies using mtDNA analysis in several species have confirmed preliminary results of stock identification or have shown differences that other methods have not detected (e.g. Avise et al., 1986; Kornfield, 1986; Hanzawa et al., 1987; Kornfield and Bogdanowicz, 1987; Ward et al., 1989).

Recently, incongruent results have been reported with mtDNA and allozymes. Ferguson et al. (1991) did not find evidence of population structure in brook char, *Salvelinus fontinalis*, using mtDNA analysis. Allozymatic variation showed, however, a significant divergence among sampled localities. Stott et al. (1992) concluded that American plaice, *Hippoglossoides platessoides*, comprise a single population in the Canadian Atlantic coast; mtDNA analysis gave less resolution than did allozymes. Also, Ward et al. (1994) reported that yellowfin tuna, *Thunnus albacares*, from the Pacific Ocean form at least two groups or populations according to allozyme analysis, comprising five polymorphic loci and contrasting with the homogeneity suggested by mtDNA restriction analysis.

Results obtained here could be explained by a recent population "bottleneck," which would have had a bigger effect on mtDNA than on nuclear genes (Ferris and Berg, 1987). However, it is very difficult to fix the time of such a bottleneck from allozyme data because, where a specific genetic distance value is obtained, the divergence time interval is very wide (Hillis and Moritz, 1990).

Another possible explanation lies in the population sex ratio. Birky et al. (1989) pointed out that extranuclear genes may show a more subdivided population than do nuclear genes, but this feature can be reversed if females are in excess. The sex ratio in our samples indicate a skew toward females (4.8:1 in samples from Mexico and 2.7:1 from Hawaii), and data from several fishing campaigns in Baja California during 1992 and 1993 indicate consistently high female:male ratios (~5.8:1, Castro-Longoria[1]). The observed sex ratio in Baja California waters, however, is not sufficiently skewed to explain the observed difference. In accordance with Birky et al. (1989), the number of females must always be more than seven per male for nuclear genes to show more subdivision than extranuclear genes.

Because the gene flow suggested by N_em was higher than the required value to prevent differentiation due to genetic drift, the third alternative explanation could be some kind of selection. In our case, the hypothesis is that selection supported a significant heterogeneity in the face of genetic flow. The proof of this hypothesis is beyond the scope of this paper. In accordance with Lewontin (1991), it is not possible to discriminate between selectionism and neutralism with static-type data such as ours.

For fishery management purposes, it is important to establish clearly the presence or absence of genetic differentiation of fishery resources among geo-

[1] Castro-Longoria, R. 1994. Universidad de Sonora, CICTUS, Rosales y Niños Héroes s/n., Hermosillo, Sonora, México. Personal commun.

graphic areas. It is widely agreed that the absence of genetic differences, as suggested by allozyme analysis, cannot be attributed to genetic identity at the DNA level (Utter et al., 1987). When differences are evident from allozyme analysis, however, the possibility of population differentiation exists to some degree. According to our results, the genetic population structure of swordfish in the North Pacific is more complicated than previously shown by Chow (1994) and Grijalva-Chon et al. (1994). From the fishery resources management point of view, it is necessary to corroborate the status of swordfish populations throughout the Pacific Ocean both with a DNA-based character set and with allozyme analysis. Moreover, future studies should include a sampling strategy that analyzes temporal variation.

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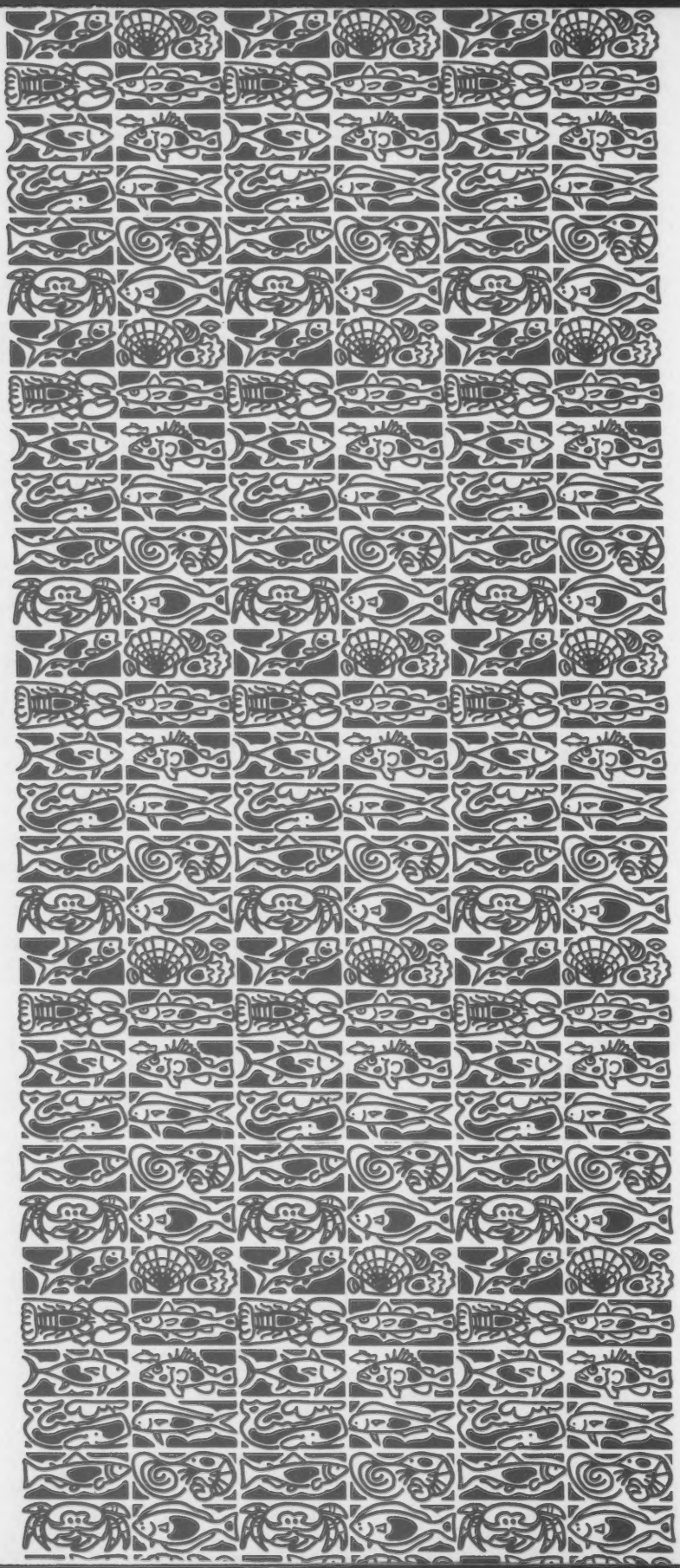
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